## The Effects of Physical Factors on the Structure of Communities

Sébastien M. J. Portalier

Doctor of Philosophy

Department of Biology

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#### ABSTRACT

A large part of studies in community ecology focus on species interactions, while the role played by the surrounding medium is often neglected. The physical components of the medium create mechanical constraints on species at the individual level. These constraints affect all organisms, from primary producers such as phytoplankton that need to stay in the light zone, up to predators that need to move to find prey. Moreover, effects of these factors potentially cascade throughout the whole food chain. These effects are size-related, and they exist across any type of ecosystem. The present thesis investigates how these mechanical constraints affect community structure at any trophic level across a wide range of body sizes. In Chapter 2, I focus on primary producers, represented by phytoplankton. Phytoplankton species are prone to sinking due to the interplay between gravity, medium density, body density, and medium viscosity. Light availability decreases with depth and turbulent mixing affects particles in the water column. I show that phytoplankton cells can persist within a size-dependent range of turbulence, and above a size-dependent critical depth. In Chapter 3, I investigate how predator-prey relationship is constrained by gravity, density and viscosity for a wide range of predator and prey body sizes, in aquatic and terrestrial systems. A predator needs to search, capture and handle prey, which leads to energy expenditure. Predation processes limit the range of prey sizes that a predator can consume. Upper prey size is determined by predator ability to capture a prey (a mechanical limit), while lower prey size is determined

by energetic costs (mostly related to handling). Lastly, Chapter 4 investigates how these factors affect the size structure and dynamics of food web modules. I show that consumer size drives the dynamics of predator-prey systems. Larger predators usually outcompete smaller predators, while smaller prey usually outcompete larger prey. Predicted predator-prey body size ratios are consistent with existing data. This thesis tries to deduce species persistence and interactions from mechanical constraints due to the medium, across a wide range of body sizes. This thesis provides novel insights on community ecology by linking the biological and physical components of ecosystems, thus going back to the roots of the ecosystem concept.

## RÉSUMÉ

Une grande partie des études en écologie des communautés se concentrent sur les interactions entre espèces, alors que le rôle joué par le milieu environnant est souvent négligé. Les composants physiques du milieu créent des contraintes mécaniques sur les espèces au niveau des individus. Ces contraintes affectent tous les organismes, depuis les producteurs primaires comme le phytoplancton qui a besoin de rester dans la zone éclairée, jusqu'aux prédateurs qui ont besoin de se mouvoir pour trouver une proie. De plus, les effets de ces facteurs peuvent potentiellement agir en cascade le long de la chaîne trophique. Ces effets sont liés à la taille des organismes, et existent dans tous les types d'écosystèmes. Cette thèse étudie la façon dont ces contraintes mécaniques affectent la structure des communautés à chaque niveau trophique, pour un vaste éventail de tailles d'organismes. Dans le Chapitre 2, je me concentre sur les producteurs primaires, représentés par le phytoplancton. Les espèces de phytoplancton ont tendance à couler à cause de l'interaction entre la gravité, la densité du milieu, la densité de l'organisme et la viscosité du milieu. La disponibilité en lumière diminue avec la profondeur et un mélange turbulent affecte les particules dans la colonne d'eau. Je montre que les cellules de phytoplancton peuvent persister dans une gamme de turbulence dépendante de la taille, et au-dessus d'une profondeur critique également dépendante de la taille. Dans le Chapitre 3, j'étudie la façon dont la relation prédateur-proie est contrainte par la gravité, la densité et la viscosité pour une vaste gamme de tailles d'organismes pour le prédateur et la proie, dans

les système aquatiques et terrestres. Un prédateur doit chercher, capturer et maintenir une proie, ce qui génère des dépenses énergétiques. Les processus de prédation limitent la gamme de tailles de proies qu'un prédateur peut consommer. La taille supérieure de proie est déterminée par la capacité de capture de la proie (une limite mécanique), alors que la taille inférieure de proie est déterminée par des coûts énergétiques (essentiellement liés au maintien de la proie). Enfin, le Chapitre 4 étudie la façon dont ces facteurs affectent la structure de tailles et la dynamique de modules de réseaux trophiques. Je montre que la taille des consommateurs dirige la dynamique des systèmes prédateur-proie. Les prédateurs plus grands excluent habituellement les prédateurs plus petits, alors que les proies plus petites excluent habituellement les proies plus grandes. Les ratios prédits de tailles prédateur-proie sont en accord avec les données existantes. Cette thèse tente de déduire la persistance des espèces et leurs interactions à partir de contraintes mécaniques dues au milieu, pour un large éventail de tailles d'organismes. Cette thèse apporte un nouvel éclairage sur l'écologie des communautés en liant les composantes biologiques et physiques des écosystèmes, revenant ainsi aux racines même du concept d'écosystème.

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#### PREFACE

### **Contribution of Authors**

The research contained in this thesis is predominantly my own. I primarily developed the research questions; defined the equations for the models; gathered data to either estimate parameters or test predictions from the models; implemented the different models; performed simulations and analytical explorations; and wrote the corresponding manuscripts.

Michel Loreau, Gregor Fussmann and Mehdi Cherif were involved in all stages of all chapters. Due to his expertise on partial differential equations and the use of Matlab, Lai Zhang helped me implement the Crank-Nicholson algorithm for Chapter 2. He also gave helpful comments to reply to some specific questions from the reviewers during revision of the corresponding manuscript. Thus, he is co-author on this article.

My co-authors have given me their permission to include all the chapters associated with their name to my thesis.

#### Thesis Format and Style

The present thesis is written in a manuscript-based format. It includes three research chapters for which I am the leading author. In order to make the thesis coherent as a whole, I included connecting statements between chapters. Since each research chapter includes a review of the literature, the first chapter will be a general introduction to the whole thesis. Each of the different research chapters have been formatted for the journal that was targeted. Therefore, the internal structure slightly varies from chapter to another. However, in order to keep some consistency throughout the whole thesis, citation style and bibliography are formatted using the style of the journal *Ecology Letters* for all chapters.

#### Statement of Originality

The manuscripts contained in the present thesis (Chapters 2-4) are novel contributions to scientific knowledge in the field of ecology, and especially in community ecology and ecosystem ecology. They consider how size-related physical factors (essentially mechanical) from the medium affect communities at each trophic level. Chapter 2 explores communities of primary producers, represented by phytoplankton. Here, I show how the size-related effects of gravity, density, viscosity, light and turbulence can affect phytoplankton persistence. The chapter expends on results from former studies i) by deriving species parameters from biological and physical laws, and ii) by considering a wide range of cell sizes. It shows that the optimal range of turbulence allowing persistence and critical depth is size-dependent.

Chapter 3 focuses on consumers and explores predator-prey relationships. The model that I introduce allows for the calculation of energetic gains and costs related to predation. It shows which interactions are feasible under the model assumptions, which costs are the most constraining for predators, and it gives insights into how predators can overcome these constraints. All patterns are consistent with real data. The model derives trophic interactions from parameters estimated at the individual level and allows predictions for aquatic and terrestrial systems, over a wide range of body sizes.

Chapter 4 integrates methods from chapter 2 and 3, and it explores food web modules. Primary producers are described using equations from Chapter 2, and consumers are described using equations from Chapter 3. I use a dynamic model based on ordinary differential equations. The model provides insights about the size structure of food web. Especially, the model shows how size affects persistence and stability of basic modules. It also informs the theoretically expected size-structure of classical modules from a one predator - one prey system up to a food chain.

Chapter 2 was published in *Ecological Modelling*. Chapter 3 is currently in revision before resubmission. Chapter 4 will soon be submitted to *Journal of Theoretical Biology*.

# Chapter 1

General introduction

#### 1.1 The medium as part of ecosystems

When Tansley coined the term "ecosystem", he also claimed that "though the organisms may claim our prime interest, when we are trying to think fundamentally, we cannot separate them from their special environments, with which they form one physical system" (Tansley, 1935). Hence, the study of living species does not really make sense without considering the medium within which they live and evolve. However, ecological studies usually focus on species, and the surrounding medium is often treated implicitly. This trend began in early studies in ecology. When Elton (1927) coined the concept of food chain and the pyramid of numbers, or when Lindeman (1942) described a lake food web as a network of species, where energy and matter circulate between compartments, the focus is clearly on species interacting with each other, and the medium is either omitted or reduced to one chemical dimension (called "ooze").

This trend is also present in later developments of the ecosystem concept. In his well known textbook, Odum (1953) popularized the concept of the ecosystem and emphasized the relationship between species and the abiotic medium. But this link involves mostly chemical elements that play a fundamental role in species' growth. The geochemical cycle of elements and the central role played by recycling processes were described as an essential component of ecosystem. However, physical factors such as gravity or density were mostly ignored.

Actually, the chemical aspect of the medium has received much more attention that its physical properties. It is well-known that species are limited by chemical elements such as nitrogen or phosphorus since the pioneering work by Liebig (1841). Numerous studies, either empirical or theoretical, have been conducted to elucidate the role played by chemical elements on community structure (Urabe & Watanabe, 1992; Elser *et al.*, 2000, 2003, 2007), which has led to the concept of ecological stoichiometry (Sterner & Elser, 2002). The fact that nutrients can be recycled or may diffuse from the sediment has also generated another body of literature (e.g., Diehl (2002); Leroux & Loreau (2010)).

The physics of the surrounding medium are either treated as very abstract way or in a very detailed way at the level of the organism. In the first approach, the medium is often viewed as a space or a volume that bounds the system of interest, such as a pond or a forest. Studies in meta-populations and metacommunities usually define a set of connected patches (Levins, 1969; Hanski, 1998; Leibold *et al.*, 2004), but the medium does not play any significant role. The medium can also be considered only from the climatic point of view (such as temperature and precipitation) that constrains species presence (Staniczenko *et al.*, 2017). Although these aspects of the medium play important roles, they do not really consider the physical aspect of the medium.

But, these factors are present in all media and constrain a large part of the species' activities. Primary producers need light for photosynthesis, thus light availability plays an essential role especially in aquatic systems where photosynthesis becomes impossible below a given depth. Foraging species are also submitted to constraints from the physical medium (such as gravity, density or viscosity). Thus, the way species interact with the surrounding medium constrains their realized niche (McGill *et al.*, 2006) and should receive more attention. Another important factor is that discrepancies exist between aquatic and terrestrial systems. Many studies emphasize these differences. The strength of trophic cascade differs between aquatic and terrestrial systems (Strong, 1992). Aquatic food webs seem to be more size-structured than terrestrial systems (Shurin *et al.*, 2006). Similarly, it seems that predators are on average much bigger than their prey in aquatic rather than in terrestrial ecosystems (Loeuille & Loreau, 2010). Models including physical factors might account for some of the differences among communities and lead to novel predictions (Loreau, 2010), a guiding theme also of this thesis.

A number of studies took the second approach, considering the medium in a very detailed way. These studies have considered the effects of physical factors on biological organisms. Some of these studies focused on specific aspect of species persistence, such as survival in turbulent waters (Denny *et al.*, 1985; Koehl & Alberte, 1988). Other studies investigated effects of physical factors on feeding constraints (Rubenstein & Koehl, 1977; Koehl & Strickier, 1981), or the mechanical constraints that might have affected evolution of specific structures, such as wings (Kingsolver & Koehl, 1994). These studies have led to very detailed models that provided important insights into animal locomotion (Cheer & Koehl, 1987; Dickinson *et al.*, 2000). On the flip side, it is challenging to generalize these models across a wide range of sizes and media, as well as to derive their implications on the dynamics of the complex communities in which the organisms studied are embedded.

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The present thesis focuses on physical constraints acting on species persistence and interactions in pelagic and aerial systems, and considers the whole natural size spectrum of organisms on Earth. The work presented here forms a midpoint between the two aforementioned approaches, being neither too abstract, nor too specific: the models start from first principles of mechanical laws but avoid going into too much detail that would prevent generalization across sizes. Similarly, models presented here include well-known biological aspects related to size, but without reaching the level of details of energy budget models (Yodzis & Innes, 1992) in order to avoid excessive complexity. This relative parcimony allows the models built in this thesis to be general enough to stay valid across sizes and media.

The aim of the thesis is to investigate the role that the surrounding medium plays in structuring organismal communities. The models used in this thesis explicitly consider mechanical constraints acting on organisms so that they can be mathematical vehicles of the general approach chosen here, which emphasizes the interplay between organisms and their surrounding medium. As such, the thesis highlights the role played by the medium as a major driver for species persistence, species interactions, and its importance in shaping the size-structure of communities. In a context of global warming, physical features of the medium may be modified; the present thesis provides a framework that may be used to investigate potential effects of global warming on ecosystems and the size-structure within communities. The thesis also emphasizes the need to include physical aspects of the medium in ecological studies (either empirical or theoretical).

#### 1.2 Body size

Physical factors affect organisms. More precisely, they primarily affect their organismal body. Hence, effects of these factors are related to body size. For example, a larger body size correlates with a greater mass, which leads to a greater weight due to gravity. Throughout this thesis, body size is the main descriptor for species characteristics. All chapters investigate a specific aspect of the size structure of communities. The rationale of the choice of body size as a master trait rests upon the fact that many biological traits are size-dependent. Hence, many biological parameters, such as metabolism or lifespan, scale with body size (Peters, 1986; Savage *et al.*, 2004). For primary producers, size is a fundamental trait since other traits such as growth (Niklas & Enquist, 2001), chlorophyl content (Finkel, 2001; Baird & Suthers, 2007), or carbon content (Menden-Deuer & Lessard, 2000) are size-dependent. For consumers, the maximal mechanical force that an organism can produce scales with size (Marden & Allen, 2002).

Body size also plays a fundamental role at the population or community level. Size usually determines the type of interaction between a consumer and a consumed species, from parasitism to predation (Lafferty & Kuris, 2002). Body size ratios between predators and prey seem to be a key factor for stability of real food webs (Brose *et al.*, 2006b). And many food web models use size to sort species *a priori*, such as the cascade model (Cohen *et al.*, 1990; Solow & Beet, 1998) or the niche model (Williams & Martinez, 2000). Body size also constrains species abundance since individuals from a larger species should be less abundant than individuals from a smaller species (White *et al.*, 2007). Body size also determines the interaction between the body and the medium. E.g., effects of gravity (i.e., weight) are directly related to body mass. A body surrounded by a fluid experiences Archimedes' force and drag proportional to its volume. Effects of drag increase by several orders of magnitude when body size decreases. Hence, small organisms live in a medium where viscous forces are a major component and inertial forces are almost absent (Guasto *et al.*, 2012; Andersen *et al.*, 2015). For these organisms, motion requires a large amount of energy compared to their size.

For all these reasons, body size was chosen as a master trait to describe species. It is another aspect of the novelty of this thesis. Models provided in the thesis use parameters that for the most part are related to body size. Thus, it allows evaluating parameter values for a wide range of body sizes, instead of being limited to values from well-studied species, which leads to more general conclusions. Moreover, results derived from these models should be easily testable since size is generally easy to measure. It also allows to link separate features of a mechanism through body size. For example, theoretical studies on predator and prey dynamics usually consider one parameter at a time (e.g., the effect of an increase of attack rate or handling time), but these parameters are usually not independent from one another: a larger predator should show a greater attack rate and a lower handling time for a given prey type than a smaller predator. Thus, linking parameter values to body size accounts for this relationship and leads to more realistic conclusions.

#### 1.3 Common features of the models used throughout the thesis

The present thesis focuses on physical factors and their role on community structure. Several aspects are shared by several or all chapters. They are here defined.

#### 1.3.1 Energy

A feature that is common to all models provided throughout this thesis is energy. All models consider energy (in joules or joules/kg) or energy-related parameters. Several prior studies demonstrated a relationship between energy, predator-prey body size ratio, and food web stability (Emmerson & Raffaelli, 2004; Otto *et al.*, 2007). For primary producers, light is converted into energy stored in the biomass (Chapters 2 and 4). Predators move when they search, capture or handle their prey. This leads to energy expenditure (work) that is estimated by the models (Chapters 3 and 4) and determines the net energetic gain of predation (Chapter 3) and, therefore, the conversion efficiency of prey biomass into predator biomass (Chapter 4).

#### **1.3.2** Primary producers

Throughout this thesis, primary producers are defined as photosynthetic organisms using light (and carbon dioxide) to produce organic matter. Carbon dioxide is assumed to be non limiting. In the present thesis, primary producers are restricted to phytoplankton species. The main reason for this choice is that phytoplankton cells are a case in point for the study of physical factors (Kiørboe, 2008). In water, light availability decreases with depth. It determines a euphotic versus a dark zone (Wetzel, 2001). Phytoplankton cells are submitted to several forces (such as weight) that determine their ability to stay within the light zone. Thus, the interplay between size and physical factors is a main feature of phytoplankton persistence.

This feature is far less prevalent for terrestrial plants. Although slight variations in light absorption may occur with a change in altitude (Gale, 1972), one cannot define a light zone and a dark zone in terrestrial systems. Competition for light between terrestrial plants derives from the fact that taller plants can shade the light below them, but the mechanism is totally different from aquatic systems. Although physical factors (especially gravity) are still of primary importance for terrestrial plants (e.g. trees), the presence of specific tissue structures (e.g., sclerenchym, xylem) allow plants to counteract the effects of these physical factors. For the sake of simplicity, the present thesis focuses on aquatic primary producers that float in water (i.e., phytoplankton) and atherefore directly exposed to most physical factors.

#### **1.3.3** Predators

A predator is an organism that feeds on another organism. However, among existing species, predation may exhibit many different aspects. Predators considered throughout this thesis share common features, but they cannot represent the full extent of existing predators. My models make some simplifying assumptions. First, predators actively move while searching for their prey. Therefore, the models exclude sessile predators and filter feeders since these predators either wait for a prey or create a current (thus moving the medium) to drive the prey toward them. Second, predators consume the whole prey, not just part of the prey. They may need several bites to do so, but the whole prey is consumed. Thus, the definition excludes predators consuming only part of the prey such as some sharks or some herbivores. Third, interactions occur on a one-to-one basis, which means that one predator successively searches, captures and handles one prey at a time. Thereby, the definition excludes microphagy, where a predator consumes several prey at a time. In that case, the predator receives a large amount of energy (compared to the consumption of one prey) with a cost that is not proportional to the number of prey (since the predator spends energy to search and capture several prey objects at a time, not a single prey object). Models also exclude predators hunting in groups since these predators can cooperate together to increase the likelihood of capture, which implies specific behavioral aspects that are difficult to represent in a general model. However, microphagy and group hunting are considered in Chapter 3 to investigate which limits defined by the model are overcome by these predators.

Last, the specific case of herbivores has to be mentioned. Herbivores usually feed on organisms that do not move by themselves. Chapter 4 considers some herbivores: predators feeding on phytoplankton (such as zooplanktonic predators). But, terrestrial herbivores and aquatic herbivores feeding on large algae usually consume only part of their prey. These cases are not considered in the present thesis since they violate the assumption of total consumption of the prey (see above). They may be included in further studies.

#### **1.4** Physical factors included in the model

Throughout this thesis, physical factors are applied as forces constraining species growth (limiting energy intake) and interactions between species (predator and prey). Considering that multiple physical factors act on living species, a choice was made on whether or not a given factor should be included. Then, these factors were included in the model using a general framework valid throughout the whole thesis.

#### 1.4.1 The choice of factors

The rationale for this choice is to build the most parsimonious model that includes all essential factors without going into too much detail. Thus, the chosen factors were those that are present in every ecosystems and that directly affect species motion (Lampert & Sommer, 1997).

The first factor is gravity, which results in the weight force. Every organism has a weight, whatever the medium is it lives in. The second factor is density. Medium density and body density determine if an organism is naturally buoyant in its surrounding medium. The volume of medium equivalent to organismal body volume, which is displaced by this body, determines the Archimedes' force that works in opposite direction to weight. The third factor considered is medium viscosity. Medium density and viscosity are major components of drag. Except in vacuum, any moving body faces an opposite force due to the resistance of the medium against this motion, which is called drag. For the sake of simplicity, only surface drag is considered.

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Light availability is also included in Chapters 2 and 4 since light is of primary importance for photosynthetic species. Especially, light distribution throughout the water column is a fundamental limiting factor in aquatic systems. Last, in Chapter 2, turbulent mixing was included. Mixing of the water column is a fundamental process for phytoplankton since it may allow or prevent species persistence (Riley *et al.*, 1949). However, the relationship between turbulence and body size is far from obvious. Thus, turbulence was assumed to be homogenous for all phytoplankton species, as it is commonly assumed in the literature (Huisman *et al.*, 1999a; Yoshiyama *et al.*, 2009; Mellard *et al.*, 2011).

Several factors have been discarded. The most important ones are temperature and water availability. These two factors are known to play a major role in terrestrial systems. They usually constrain presence or absence of a species in a given ecosystem. Thus, models such as energy budget models (Kearney & Porter, 2009) consider temperature and water availability to predict species niches. These factors are also the main drivers of biome boundaries (Whittaker, 1975). However, these two factors were discarded for several reasons. First, temperature and water have several effects on organisms, and these effects are not unambiguous as they may affect species growth or activity in multiple ways (Angilletta *et al.*, 2004; Levy *et al.*, 2016). Moreover, these effects are poorly related with body size, which is the other cornerstone of the present thesis. Second, water availability is constraining only for terrestrial species, but not in aquatic systems. Last, temperature also affects the physical properties of the medium since both density and viscosity vary with temperature (see tables 1–1 and 1–2). Temperature related to latitude may also play a role for species body size. Although criticized, Bergmann's rule argues that within clades, larger species should be found in colder environments (Blackburn *et al.*, 1999; Meiri & Dayan, 2003). Thus, inclusion of temperature would have raised too many issues that would have prevented a clear understanding of the mechanism and the conclusions of this thesis.

Therefore, the present study assumes a constant temperature for the medium, and no water limitation for terrestrial species. The model presented here tries to be the most parsimonious one and only includes physical factors that are always present in the medium. Other potential factors are assumed constant or not limiting. Adding more factors from the beginning might have weakened the generality of the results. But the model is flexible enough to allow for future extensions by considering factors that were discarded at first glance.

#### 1.4.2 Inclusion of physical factors in the calculation of parameters

One aspect of the novelty of this thesis is the fact that parameters used in the different models were not derived empirically from studied species. All calculations use classical biological rules and basic Newtonian physics and fluid mechanics that are related to body size. Thus, these models are valid for a wide range of sizes, which lead to more general predictions. Mechanical factors related to the medium (i.e., gravity, density and viscosity) are included within forces that ultimately lead to the calculation of a motion speed. Light is a different factor and is treated separately (see below). Gravity, density and viscosity constrain the hovering and motion of species.

Hovering is the ability to stay at a given vertical position (e.g., depth or altitude). In Chapters 2 and 4, phytoplankton cells do not hover. They have a passive sinking velocity since they do not move by themselves. For all species, this sinking velocity results from the interplay between several forces. The first force is weight and acts downwards. The second force is a reaction force due to fluid density and known as Archimedes' force, acting upwards. The third and last force is drag, and it always acts in opposite direction from that of motion. The physical factors are included within these three forces: gravity is part of weight, medium density is part of Archimedes' force and drag, and medium viscosity is part of drag. Body density makes the connection between body mass (acting on weight) and body volume (acting on Archimedes' force).

Predators and moving prey (Chapters 3 and 4) actively move within the medium. More precisely, motion is represented as an oscillatory movement (Bejan & Marden, 2006). A species' active motion is split between two components: a vertical and a horizontal one. The vertical one is similar to the sinking velocity described above, but these organisms spend energy during motion to maintain an active hovering: the model assumes that they manage to stay at the same depth or altitude. In other words, they actively counteract their natural sinking velocity. A fourth force is added to the three forces described above: a muscular force (thrust). The horizontal component includes a muscular force (thrust) and drag acting in opposite directions. All these forces (weight, Archimedes' force, drag, thrust) are added together and determine an overall force. According to Newton's second law, force divided by mass leads to acceleration, which is the first derivative of speed with respect to time. Thus, the calculation ultimately leads to a sinking speed (for phytoplankton species) or motion speed (for moving species).

The last physical factor, light availability, plays a major role in photosynthesis. It is included into gross photosynthetic production (Chapter 2 and 4). A constant irradiance represents light entering at the top of the ecosystem. This light is absorbed either by photosynthetic species or by the medium, following Beer-Lambert's law (Huisman & Sommeijer, 2002b). Cells compete for light. In Chapter 2, since depth is explicitly included, light availability determines a light zone and dark zone.

#### 1.5 Scope of the thesis

The models built in the present thesis share several assumptions. The main assumption is that organisms spend most of their life in the water column or air column, which makes the models particularly well-suited for pelagic or flying organisms. Water column and air column share several features that make models relatively easy to implement. The column is an open medium, which means that neither prey nor predator predator can hide. Organisms also need to spend energy to hover while moving. Models representing organisms living on the bottom of the system (e.g., benthic organisms) would need to include different energetic costs (predators do not need to hover), and complex behaviours for search and capture (e.g., building traps, hiding). These additions would lead to more complex models and more complex patterns. They may be considered for further improvements.

Another important assumption is that bodies are assumed to be spherical. The main reason for this choice is that mechanical constraints acting on a sphere can be easily calculated. We are aware that morphology can affect the interaction of species with one another and with the environment (Koehl, 1996). The general philosophy of this thesis is to employ models that are relatively generic and to avoid over-specification. We believe our approach is sufficiently flexible so that models can be extended to serve as a template for more specialized species-species and species-environment interactions. On the other hand, despite — or because of — the simplifying assumptions we make, this thesis provides conclusions that are valid for many species and many ecosystems, especially for aquatic systems that are the core of most research chapters.

#### 1.6 Chapters overview

Throughout this thesis, I investigate, through a modelling approach, the effects of some physical factors on communities. Body size plays a central role in this thesis, since several biological parameters scale with size, and processes such as motion involve an interplay between physical factors and size. Each research question is related to organismal sizes, and models investigate a wide range of body sizes. Physical factors constrain all species, at any trophic level, and in all media. It appears that primary producers in aquatic systems are potentially limited by their ability to stay in the light zone of the water column. Any constraint on primary producers is likely to affect the whole trophic chain. Consumers are also affected by physical factors that constrain existence of trophic links, predator-prey dynamics, and persistence of food web modules (fig 1–1).

Chapter 2 studies the effects of physical factors on phytoplankton communities, with a focus on the bloom period. To persist, a phytoplankton species has to stay within the light zone as much as possible. However, most species are prone to sinking due to gravity. Photosynthetic yield and light requirement for maximal growth are size-dependent, as well as sinking velocity. Turbulent mixing can counteract or reinforce the sinking process. Several studies emphasized the role of turbulence in persistence of sinking-prone phytoplankton species (Huisman et al., 1999a, 2002; Huisman & Sommeijer, 2002a,b), on critical depth (Huisman et al., 1999b), and on competition between phytoplankton species (Huisman et al., 2004). However, they often focused on a few, well-known, species. In this chapter, since parameters were estimated according to body size, I explored a wide range of sizes, from very small cyanobacteria to very large diatoms, over a large range of turbulence. I find that small species can persist at very low turbulence, while large species show a lower threshold of turbulence. But all species show an upper threshold of turbulence above which they cannot persist. Similarly, species cannot exist if they sink too deep below a critical depth (Sverdrup, 1953). Large species show a critical depth at both low and high turbulence, while small species show it only at high turbulence. Because species may or may not persist according to their size, turbulent conditions and total depth of the system are likely to have a strong influence not only on phytoplankton species but also on their consumers.

While Chapter 2 focuses on primary producers, Chapter 3 investigates consumers, especially how predator-prey relationships are affected by physical factors and size. The surrounding medium constrains species motion, including motion for predation. Former studies investigating the relationship between size and predation were mostly empirical (Emmerson & Raffaelli, 2004; Barrios-O'Neill *et al.*, 2016). Although theoretical studies provided useful insights into predator-prey relationships (Yodzis & Innes, 1992; Petchev et al., 2008), a general underpinning mechanism valid for a large range of body sizes and different ecosystems is still lacking. Furthermore, studies investigating the effects of the surrounding medium mainly focused on specific organisms (Potvin et al., 2012) or on specific elements of predation such as manoeuvrability (Domenici et al., 2011a,b). In this chapter, predation is broken down into three processes: the predator has to search, capture and handle its prey, and each process leads to energy expenditure. The predator gains energy by consuming the prey. Considering a wide range of body sizes for predators and prey, and two different media (air and water), I calculate net energetic gain for each interaction. Overall, some interactions are not possible because the predator cannot capture or handle the prey; some interactions are not sustainable because the predator spends more energy than the prey can provide; but some interactions are feasible and sustainable. Predators should be larger than their prey, and this result is even more pronounced for flying predators. Each predator feeds on a range of prey sizes that is constrained by the different costs. Lower prey size is mostly determined by energetic cost due to handling, while upper prey size is determined by a mechanical constraint due to capture (i.e., the predator cannot capture the prey). The model is well suited for pelagic and flying predators, and fits real data remarkably well. The model also allows predictions as to which constraints have to be overcome by predators to breach their prey spectrum. This study provides a novel mechanistic explanation to many empirical
patterns about predator-prey body size ratio (Emmerson & Raffaelli, 2004; Brose *et al.*, 2006a; Brose, 2010; Barrios-O'Neill *et al.*, 2016).

Chapter 4 focuses on food webs, especially on food web modules. It investigates the size-structure of food web modules in pelagic systems. Some species are primary producers, using light to produce biomass, thus using the equations for photosynthesis provided in Chapter 2. Other species are consumers (predators) described by the equations from Chapter 3. The model is a dynamic model similar to the Rosenzweig-MacArthur model (Rosenzweig & MacArthur, 1963). There is intra-specific competition for light within the phytoplankton population, leading to a carrying capacity, while the predator shows a type II functional response. This chapter studies several basic food web modules: one predator-one prey, one predator-two prey, two predators-one prey, a food chain with a basal primary producer, an intermediate predator and a top predator, and lastly a food chain with an omnivorous top predator. The simple module with one prey and one predator is also investigated analytically, which leads to novel predictions that link system stability to predator and prey sizes. I found that stability conditions are mostly driven by predator size. Predators feeding on phytoplankton are usually around  $10^5$  times larger than their prey, while top predators show a lower size ratio (around  $10^2$ ). Distributions of predicted ratios are consistent with real data. Food web modules have been studied extensively in theoretical studies (Holt, 1977; Holt et al., 1994; Holt & Lawton, 1994; Milo et al., 2002; Bascompte & Melián, 2005; Gellner et al., 2016), but parameters were poorly or not at all related to size. Therefore, these studies did not allow for investigation of the size-structure of food webs. This chapter gives novel insights into the causes of size-structure since parameters are related to size and physical factors. Thus, the model provides easily testable hypotheses.

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T (C)	Density $(\rho_m)$ (kg.m <sup>-3</sup> )		
	Air	Freshwater	Seawater $(S = 35)$
0	1.293	99.87	1028.11
3.98	1.274	1000.0	1027.77
10	1.247	999.73	1026.95
20	1.205	998.23	1024.76
30	1.165	995.68	1021.73
40	1.128	992.22	1017.97

Table 1–1: Medium density in different media according to temperature (Denny, 1993)

T(C)	Dynamic viscosity ( $\mu$ ) (N.s.m <sup>-2</sup> )				
	Dry Air	Freshwater	Seawater $(S = 35)$		
0	$1.718.10^{-5}$	$1.79.10^{-3}$	$1.89.10^{-3}$		
10	$1.768.10^{-5}$	$1.31.10^{-3}$	$1.39.10^{-3}$		
20	$1.818.10^{-5}$	$1.01.10^{-3}$	$1.09.10^{-3}$		
30	$1.866.10^{-5}$	$0.80.10^{-3}$	$0.87.10^{-3}$		
40	$1.914.10^{-5}$	$0.65.10^{-3}$	$0.71.10^{-3}$		

Table 1–2: Medium dynamic viscosity in different media according to temperature (Denny, 1993)



Figure 1–1: Thesis outline. In Chapter 2, phytoplankton cells show a sinking velocity resulting from the difference between weight, Archimedes' force and drag. They need light for photosynthesis and experience turbulent mixing. In Chapter 3, predators actively move to search, capture and handle prey. Motion is represented as an oscillatory process. In Chapter 4, phytoplankton cells are eaten by consumers, which may themselves be consumed by other predators. Several food web modules are investigated.

### Connective statement # 1

Most ecosystems rely on the solar energy fixed by photosynthetic organisms. Thus, these species represent the lowest trophic level in food webs, and their relative abundance or even their presence will drive the structure and the complexity of the food web they belong to. In aquatic ecosystems, sunlight reaching the surface of a lake or ocean is quickly absorbed, and below a given depth, photosynthesis is not possible. Photosynthetic organisms (i.e., phytoplankton) should therefore stay within the light zone in order to persist. Effects of mechanical factors are of primary importance in aquatic ecosystems since many species are likely to sink into the darkness due to gravity. In Chapter 2, I investigate how mechanical factors related to size affect persistence of phytoplankton species. Cells are submitted to several mechanical factors (i.e., gravity, medium density, body density, medium viscosity, turbulent mixing), light availability, and biological factors (e.g., growth rate) that affect species persistence. This chapter gives insights into phytoplankton persistence related to size. It also provides essential information for Chapter 4 since persistence of primary producers will directly affect persistence of higher trophic levels.

## Chapter 2

# Size-related effects of physical factors on phytoplankton communities

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Portalier, Sébastien M. J.<sup>1</sup>, Cherif, Mehdi<sup>2</sup>, Zhang, Lai<sup>3</sup>, Fussmann, Gregor

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<sup>&</sup>lt;sup>1</sup> Department of Biology, McGill University

 $<sup>^2</sup>$ Department of Ecology and Envrionmental Science, Ume<br/>å University, SE-90187, Umeå, Sweden

 $<sup>^3</sup>$  Department of Mathematics and Mathematical Statistics, Umeå University, SE-90187, Umeå, Sweden

<sup>&</sup>lt;sup>4</sup> Centre for Biodiversity Theory and Modelling, Station d'Ecologie Expérimentale du CNRS, 09200 Moulis, France

#### 2.1 Abstract

Phytoplankton communities are influenced by light availability. Therefore, one factor promoting phytoplankton species persistence is their ability to stay within the euphotic zone. This ability is determined by the interplay between species mass, buoyancy and dispersion, which are driven by physical factors. In this study, we investigate how these physical factors and light-use efficiency, all correlated with cell size, influence species persistence. Our model shows, first, that species can persist only within a size-dependent range of turbulence strength. The minimal level of turbulence required for persistence increases drastically with cell size, while all species reach similar maximal levels of turbulence. Second, the maximal water column depth allowing persistence is also size-dependent: large cells show a maximal depth at both low and high turbulence strength, while small cells show this pattern only at high turbulence strength. This study emphasizes the importance of the physical medium in ecosystems and its interplay with cell size for phytoplankton dynamics and bloom condition.

Keywords: turbulence, light limitation, critical depth, phytoplankton bloom

#### 2.2 Introduction

Light is an essential resource for primary producers. Light distribution over the planet controls primary production over large tracts of the planet's oceans and lakes. Especially, light is a limiting resource during spring blooms. Since these blooms are responsible for a disproportionate fraction of the annual aquatic primary production (Parsons *et al.*, 1984), and of the carbon pump (Watson *et al.*, 1991; Sanders *et al.*, 2014), their study is of primary importance. However, despite decades of studies, the conditions and factors affecting the onset, magnitude and species composition of spring blooms are still debated (Townsend *et al.*, 1994; Behrenfeld & Boss, 2014; Daniels *et al.*, 2015). Indeed, the phytoplankton requires light for growth, but light availability in the sea and in lakes decreases with depth. To persist, phytoplankton populations must stay in the upper region of the water column, known as the euphotic zone, where light availability is sufficiently high to sustain positive population growth rates.

Early work identified turbulent mixing of the water column (or turbulence) as a key factor contributing to the persistence of phytoplankton populations (Riley et al., 1949) and described the interplay of turbulence and light-dependent growth in sinking-prone phytoplankton species (Shigesada & Okubo, 1981; O'Brien et al., 2003). Indeed, the density of many phytoplankton species is higher than that of the surrounding medium, which means they are prone to sinking under the effects of gravity (Smayda, 1970; Reynolds, 2006). Hence, phytoplankton species need to passively or actively counteract the effects of gravity. Several phytoplankton species can actively decrease their body density and increase their buoyancy, e.g., through gas vacuoles or lipids (Waite, 1992; Waite et al., 1992), which especially allows large phytoplankton species to persist in the water column (Villareal, 1992). Margalef (1978) studied how sinking velocity, turbulence, grazing, nutrients and light availability can constrain phytoplankton adaptations, and Sverdrup (1953) argued that systems deeper than a critical depth cannot sustain algal blooms. More recently, Huisman & Sommeijer (2002b) proposed a model that includes turbulence, sinking velocity and light-dependent growth of

the phytoplankton. They demonstrated that only intermediate turbulence allows sinking phytoplankton species to persist. If turbulence is too low, individuals sink too fast, whereas if turbulence is too strong, individuals do not spend enough time in the euphotic zone. In both cases, the population cannot persist.

Therefore, it seems clear now that hydrodynamical forces may play a major role in the size structure of phytoplankton (Rodríguez et al., 2001). Hence, the ability of a phytoplankton species to grow under light limitation depends on the complex interplay between its growth rate, mortality rate, photosynthetic capacities, sinking properties and turbulent diffusivity. However, these properties are quite disparate and often hard to measure, particularly *in situ*. Some studies investigated the interplay between sinking velocity and persistence (Huisman & Sommeijer, 2002a), but growth and sinking velocity were totally decoupled, while they should be related to each other, as indicated by recent works showing that most of these properties are underlined by a master trait: size (Edwards *et al.*, 2015). Yet, it should be possible to derive estimates for most of these properties based on the cell size of organisms and on the physical properties of the medium in which they live. The laws of physics dictate that cell size in interaction with turbulence and gravity will be key factors for phytoplankton persistence. For example, a large, heavy phytoplankton individual will be more prone to sinking than a small, light one because of differences in the interplay between gravity, medium density, body density and drag. Effects of differential sedimentation due to size differences have been investigated for particles in marine waters (Li et al., 2004), but not for living cells.

In this study, we investigate the importance of body size on phytoplankton species persistence, determined by (a) the interplay between a species' physical and biological properties, and (b) the properties of the medium in which this species lives. Our work is the first to include size as the master trait in a vertically structured, dynamical model of phytoplankton growth under light limitation. Moreover, whenever possible, we derive the size-dependence of traits from primary physical laws, and not empirical allometries, in order to increase the generality of our approach and make it adaptable to different physical conditions. We will use the generic term "body" throughout, acknowledging the fact that the functional unit of phytoplankton in water can be a single cell or a multitude of cells forming a colony. Our first objective is to extend and generalize previous findings on phytoplankton persistence and vertical distribution to a wider range of body sizes, and thereby, to gain a more differentiated understanding of the physical conditions allowing phytoplankton species persistence. The second objective is to investigate the role of physical factors on species persistence by coupling species-specific properties (i.e., growth and motion) to physical factors of high relevance.

Many phytoplankton species show specific adaptations (e.g., gas vacuoles, mucilage) that allow them to control buoyancy Reynolds (2006). To avoid unnecessary complexity and keep our model tractable we decided not to consider buoyancy-related adaptations in the present study. First, buoyancy control might not be the only function of traits that decrease density (Reynolds, 2006). Second, species can modify their buoyancy through time, and the relationship between these adaptations and body size is complex (Moore & Villareal, 1996b,a). Third, buoyancy-related adaptations have costs (Walsby, 1994) that are not negligible. In the absence of reliable empirical data on these relationships we felt that the inclusion of buoyancy-related structures would not provide any reliable insight into which species would benefit from these adaptations. As it stands, our model considers species slightly denser than water and, thus, predicts the spatial structure of phytoplankton communities with non-actively buoyant species; as such, the model can be used to identify species that would benefit most from increasing their buoyancy.

More importantly, our model focuses on light limitation and ignores nutrient limitation. Nutrients are known to influence phytoplankton growth (Marañón *et al.*, 2013; Wirtz, 2013), and competition (Ryabov & Blasius, 2011, 2014; Kerimoglu *et al.*, 2012). However, light is an important factor and a special resource. Indeed, light is essential for photosynthesis, and its distribution through the water column is inverted compared to nutrients. During blooms light but not nutrients is most often the limiting resource. Moreover, some lakes seem to be permanently light-limited rather than nutrient-limited (Karlsson *et al.*, 2009). Last, our model assumes complete mixing of the water column. Thus, it is best suited to represent a phytoplankton species in a lake or coastal area with no thermocline, and at a time when a bloom is likely to occur.

As key physical factors of the medium, we consider light absorption, density, viscosity and turbulence, which are classical factors usually used to define the physical properties of a medium (Lampert & Sommer, 1997). Key properties of phytoplankton species living in the water column are photosynthetic rate (which,

via light availability, controls their population growth rate); body density (whose relationship to medium density determines their buoyancy); and cross-sectional area (which interacts with the medium's viscosity to create the drag forces that phytoplankton face when moving). Finally, body size is included as an explicit master trait affecting all the rates of organisms, i.e., photosynthesis, metabolic loss, natural mortality and sinking rates. This study gives new insight into the conditions allowing phytoplankton blooms at a specific cell size and turbulent regime. This work is a contribution towards a better prediction of phytoplankton growth in light-limited environments.

#### 2.3 Model Description

#### 2.3.1 General description

The model describes a phytoplankton population, in a mixed water column of depth  $Z_{max}$ . Three different processes occur. i) The first process represents biological mechanisms (such as photosynthesis, metabolism or death). These mechanisms are included in a reaction term. ii) Second, due to the interplay between the species' weight and its buoyancy, individuals are submitted to an oriented motion either toward the bottom, if they are denser than the medium, or toward the top, if they are naturally buoyant. This motion can be represented by an advection term. iii) Last, turbulence adds a new component to individual motion. However, turbulence is by definition unpredictable and unoriented. This is why turbulence is represented by a diffusion term. Therefore, the model is written as a reaction-advection-diffusion model (see table 1 for a list of parameters)

$$\frac{\partial\omega}{\partial t} = R(z,t)\omega - v\frac{\partial\omega}{\partial z} + D\frac{\partial^2\omega}{\partial z^2}$$
(2.1)

where  $\omega$  is the population abundance at depth z, R is the overall growth rate per capita (the reaction), v is the sinking velocity (the advection), and D is the diffusion due to turbulence. Each term is calculated according to the biological and physical properties of the species, and their interplay with physical factors of the medium.

#### 2.3.2 The reaction term

The reaction term represents the growth rate *per capita*, and it depends on four different mechanisms. The first one is photosynthesis (P), which varies according to light availability  $(I_z)$  at each depth. It describes the amount of energy gained by photosynthesis. However, photosynthesis has a cost, due to pigments synthesis, which is represented by the second term  $(P_c)$ . The third term represents loss through basic metabolism (m). The last term represents loss though natural death of the organisms  $(l_d)$ .

$$R(z,t) = P(I_z) - P_c - m - l_d$$
(2.2)

The first term, the photosynthesis rate (P), is a saturating function of the rate of photons captured by an organism (Finkel *et al.*, 2004)

$$P(I_z) = P_{max} \tanh\left(\frac{a\phi I_z}{P_{max}}\right)$$
(2.3)

where  $I_z$  is the irradiance at depth z and time t,  $P_{max}$  is the maximal photosynthetic rate, a is the absorption cross-section, and  $\phi$  is the quantum yield of photosynthesis. It appears that  $P(I_z)$  is a saturating function of  $I_z$ . Both maximal photosynthetic rate  $(P_{max})$  and absorption cross-section (a) are functions of body size (Finkel & Irwin, 2001)

$$P_{max} = k_{max} \left(\frac{V_b}{V_{0p}}\right)^{0.75} \tag{2.4}$$

where  $k_{max}$  is the maximal photosynthetic rate at reference size  $(7.75*10^{-18} \text{ mol C.s}^{-1})$ ,  $V_b$  is body volume, and  $V_{0p}$  is the volume at reference size  $(3.35*10^{-17} \text{ m}^3)$ .  $k_{max}$  and  $V_0$  are estimated for a *Chlorella* cell Reynolds (1990). The absorption crosssection (a) is calculated following Finkel *et al.* (2004) (see appendix A for details). It increases with body size.

The second term of the reaction equation is the photosynthetic cost term  $(P_c)$ 

$$P_c = \frac{cV_b\zeta\phi}{\tau} \tag{2.5}$$

where  $\zeta$  is the cost of photosynthetic apparatus,  $\tau$  is the average lifetime of this apparatus over which the cost of this apparatus is amortized,  $V_b$  is cell volume, and c is chlorophyll a content *per cell* (see appendix A for details).

Units for the photosynthetic rate (P) and photosynthetic cost  $(P_c)$  are mol C.s<sup>-1</sup>. In order to transform these molar rates into *per capita* rates, both values are multiplied by the molar weight of carbon (12 g. mol C<sup>-1</sup>). Then, they are divided by the amount of carbon needed to produce one individual  $(C_b)$ (Menden-Deuer & Lessard, 2000).

$$C_b = C_0 \left(\frac{V_b}{V_{0C}}\right)^{0.88} \tag{2.6}$$

where  $C_0$  is carbon content at reference size (set at 2.6 \* 10<sup>-13</sup> g C), and  $V_{0C}$  is volume at reference size (set at 10<sup>-18</sup>m<sup>3</sup>). Hence, the net *per capita* growth due to photosynthesis decreases when body size increases.

The third term is the metabolic rate (m), which increases with body size Peters (1986)

$$m = 0.01 \ M_h^{0.75} \tag{2.7}$$

where  $M_b$  is body mass (in kg) and m is the metabolic loss (in J.s<sup>-1</sup>). This energetic rate is then divided by the amount of energy contained within one individual (*E*).

$$E = M_b R_{dw} E_{dw} \tag{2.8}$$

where  $M_b$  is the body mass (wet mass),  $R_{dw}$  is the ratio between the dry ash-free mass and the wet mass, and  $E_{dw}$  is the ratio of energy to dry mass. Overall, *per capita* metabolic rate increases with body size.

The last term is *per capita* loss by natural death  $(l_d)$ . This natural death rate, excluding external source of death (e.g., predation), is assumed to be the inverse of life span, which scales with body size McCoy & Gillooly (2008)

$$l_d = l_{0d} * \left(\frac{M_b R_{dw}}{V_{0d}}\right)^{-0.22}$$
(2.9)

where  $l_{0d}$  is death rate at reference size (set at  $1.58 * 10^{-6} \text{ s}^{-1}$ ), and  $V_{0d}$  is reference size (set at  $1.08 * 10^{-15} \text{ m}^3$ ). The overall *per capita* growth rate calculated is in accordance with empirical observations (Finkel *et al.*, 2010).

An overview of the four parameters considered (i.e., photosynthetic gain, photosynthetic cost, metabolic cost, death loss) leads to the following conclusion:

for a given size, the costs  $(P_C, m, \text{ and } l_d)$  are constant, and the reaction term varies with light availability  $(I_z)$  at each depth. Light availability follows a Beer-Lambert's law (Huisman *et al.*, 2004), and therefore, depends on light absorption by populations above the considered depth z and the background absorption (i.e., water turbidity)

$$I_z = I_0 \exp\left\{-\int_0^z a\omega(\sigma, t)d\sigma - K_{gb}z\right\}$$
(2.10)

where  $I_0$  is the initial irradiance received on the top of the system (in mol photon.s<sup>-1</sup>), a is absorption cross-section (defined above),  $\sigma$  is an integration variable, and  $K_{bg}$ is the background absorption by water and other components than phytoplankton (in m<sup>-1</sup>).

#### 2.3.3 The advection term

The advection term represents the average sinking velocity of a single organism. It evaluates the relative importance of an organism's weight and buoyancy. Therefore, it is oriented either downwards, if the species is denser than the medium, or upwards, if the species is naturally buoyant. Due to their small size, phytoplankton species are usually assumed to be located below the Kolmogorov scale, so that sinking velocity can be calculated using Stokes' law (Davey & Walsby, 1985; Fogg, 1991). However, some phytoplankton species are large enough to face conditions above the Kolmogorov scale (Lazier & Mann, 1989), where Stokes' law is not valid anymore (Almedeij, 2008). Therefore, we use a more general method that can be used either below or above the Kolmogorov scale. A sinking force (F) is calculated, including as its terms three forces that act constantly on organisms. The first term represents weight (i.e., the effect of gravity on the body) and is oriented downwards. The second term represents buoyancy (i.e., Archimedes' force) and is oriented upwards. Considering that motion does not occur in a vacuum, the viscosity of the medium also plays a role. Hence, the last term represents drag (i.e., the effect of medium viscosity) and is always opposed to motion. This model considers only one component of drag, which is surface drag

$$F = gM_b - V_b\rho_m g - \frac{1}{2}S_b v^2 \rho_m C_d$$
 (2.11)

where g is acceleration due to gravity,  $\rho_m$  is medium density, v is speed,  $S_b$  is the body section surface, and  $C_d$  is the drag coefficient. Then, this equation allows the calculation of an equilibrium speed, which is the sinking velocity (see appendix B for details). Sinking velocity increases with body size, which is in accordance with empirical observations (Kiørboe, 2008). If Reynolds' number becomes very low (i.e.,  $Re \ll 1$ ), the last term of equation B.2.18 dominates (see appendix B), which leads to similar results as with Stokes' drag coefficient. However, while Stokes' law is valid only for very low Reynolds' numbers, our approach is more general and allows prediction of sinking velocity for bigger cells or colonies that can face conditions beyond Stokes' law conditions.

#### 2.3.4 The diffusion term

Turbulence is neither predictive nor oriented. This is why turbulence effects are represented as a diffusion process. The current of fluid produces a force on cells, leading to motion. This motion can be easily included into a diffusion parameter. In order to avoid confusion with other definitions of diffusion (e.g., molecular diffusion), we will use the term "turbulent diffusion" throughout. However, calculating the effect of current speed on the diffusion parameter value according to organism body size remains challenging. Moreover, turbulence is a complex phenomenon that occurs at different scales. Thus, the relationship between turbulence and diffusion related to body size remains difficult to describe precisely. Many studies have investigated the effects of turbulence on predation rate (Lewis & Pedley, 2000, 2001), nutrient uptake (Metcalfe et al., 2004; Hondzo & Wüest, 2009), or phytoplankton patchiness (Seuront, 2005). Although the effects of turbulence on plankton settling rate have been studied Ruiz et al. (2004), it is challenging to disentangle the relative effects of turbulence and gravity in these studies. So far, we are not aware of any study, either empirical or theoretical, that calculates the turbulent diffusion of planktonic cells according to the attributes of turbulent currents, and the relationship between this turbulent diffusion and cell body size. Previous studies considering turbulence set the turbulent diffusion parameter at a constant *ad hoc* value (Huisman *et al.*, 1999a; Huisman & Sommeijer, 2002b; Yoshiyama et al., 2009; Mellard et al., 2011), implicitly assuming that turbulence has similar effects on phytoplankton cells of different body sizes. For a lack of a better alternative, we use a similar approach. However, studies have emphasized the importance of considering the relationship between turbulence and body size (Zhang et al., 2014).

#### 2.3.5 Implementation

The system represents the mixed layer of a water column. It is assumed that no individual can enter or leave the system at the top (0) and bottom boundary layers  $(Z_{max})$ , which is a zero flux boundary condition. This case happens in lakes and shallow coastal waters during spring or fall, and this condition was used in several studies (Huisman *et al.*, 1999a; Huisman & Sommeijer, 2002b; Huisman *et al.*, 2002).

$$v\omega - D\frac{\partial\omega}{\partial z}|_{z=0} = v\omega - D\frac{\partial\omega}{\partial z}|_{z=Zmax} = 0$$
(2.12)

The model is solved numerically by using a finite volume method by Crank-Nicolson's scheme, which is known to be a very stable scheme for reactionadvection-diffusion equations in one dimension (Najafi & Hajinezhad, 2008). Finite volume method and the Crank-Nicolson scheme are commonly used in physics. Moreover, in order to check the validity of applying our method to an integro-reaction-advection-diffusion model, we also did some tests using a scheme combining the method of lines, a third order upwind scheme and the trapezoid rule, as described in detail in Huisman *et al.* (2002). Both methods give similar results. However, the method we use is computationally lighter.

Numerical model's simulations were performed with Matlab (8.0.0.783) and Java (1.6.0\_65); figures were made using the R software (R Core Team, 2013).

#### 2.4 Results

In this study, species body density is set at 1080 kg.m<sup>-3</sup>, which is the mean density value for biological organisms Denny (1993). Individuals are slightly denser than their surrounding medium, and therefore they are prone to sinking. Light availability decreases with depth, and growth is maximal close to the surface. Below a given depth (compensation depth), the remaining light does not allow photosynthetic gains to compensate for the costs, which leads to a negative growth rate. In our model, when body size increases, the maximal per capita growth rate decreases, and the sinking velocity increases. Furthermore, following Huisman & Sommeijer (2002b), incident light intensity is set at  $3.5 \times 10^{-4}$  mol photons.m<sup>-2</sup>.s<sup>-1</sup>, which is assumed to be a saturating condition at the surface.

#### 2.4.1 Relationship between persistence and turbulence

According to several studies (Denman & Gargett, 1983; MacIntyre, 1993; Huisman & Sommeijer, 2002b), phytoplankton turbulent diffusion in lakes or oceans, varies from  $10^{-7}$  m<sup>2</sup>.s<sup>-1</sup> to  $10^{-1}$  m<sup>2</sup>.s<sup>-1</sup>. In this study, turbulent diffusion varies from  $10^{-8}$  m<sup>2</sup>.s<sup>-1</sup> to 1 m<sup>2</sup>.s<sup>-1</sup>, which allows the model to include the usual conditions in natural ecosystems as well as potential extreme cases. By looking at the interplay between light availability, sinking velocity and body size, for a wide range of turbulent diffusion values, several important results appear (figure 2–1). First, at low levels of turbulence (i.e., small turbulent diffusion values), small species can persist, while larger species cannot. As body size increases, the minimal turbulence strength required for persistence increases. Second, when turbulence strength increases, part of the population is present at shallower depth, and the maximal depth reached by the population increases with turbulence strength (figure 2-2). Individuals are present deeper when turbulence increases. When the system reaches a critical depth at high turbulence, the population is mostly located in the dark zone. Therefore, it cannot persist. Above an upper threshold, the population is unable to persist. Therefore, a given species can persist only within an optimal range of turbulence.

Third, the breadth of the optimal range of turbulence allowing persistence becomes narrower with increasing body size (figure 2–1). Small species are able to persist from very low to very high diffusion rates. When body size increases, a lower limit of turbulent diffusion first appears, and this limit increases with body size. However, if strong differences exist among species at low turbulence, all species seem to reach similar upper turbulence thresholds. Last, by looking at the depth profile of the population, the model leads to a fourth interesting result. When the population persists at low levels of turbulence, individuals are located very close to the surface (figure 2–2A). However, with increasing body size, this pattern is altered, and the depth of maximal abundance is located deeper (figure 2–2D, figure 2–3).

#### 2.4.2 Relationship between depth and persistence

The critical depth concept (Sverdrup, 1953) can be applied - if the water column is deep enough that the dark zone is non negligible. Under a realistic range of turbulent strength, patterns for small and large species are different (figure 2–4). As the population is located at the surface at low turbulence strengths, a small species is not affected by ecosystem depth. On the other hand, when turbulence strength increases to a very high level, the population is able to persist only in a relatively shallow system. Beyond a critical depth, the population cannot persist above an upper threshold of turbulence for the same reason as suggested by Sverdrup (1953). Because high turbulence strength increases population spread, cells are transported into the dark zone too fast. For large species, similarly to small species, a critical depth is observed at high turbulence strength. However, a critical depth is also observed at low turbulence strength. Moreover, the critical depth at low turbulence strength is shallower than the critical depth at high turbulence strength and is close to the compensation depth. Cells that are too big to be resuspended by mixing, stay outside the euphotic zone.

#### 2.5 Discussion

#### 2.5.1 Size-mediated relationship between persistence and turbulence

A number of previous studies investigated the relationship between sinking velocity, turbulence, and phytoplankton persistence (Huisman & Sommeijer, 2002b,a; Huisman et al., 2002). However, in these studies cell growth and sinking velocity were treated as totally independent parameters, while our model considers one master-trait (body size) that links all these parameters together. Thus, our model leads to two important new results. First, small species are able to persist at low turbulence, while larger species are unable to do so, which is in accordance with empirical observations (Fogg, 1991). Second, all species are unable to persist beyond an upper turbulent diffusion threshold. All species seem to reach similar upper thresholds. However, this upper threshold seems to be maximal for intermediate size species. Whether these small differences are important for community structure at high turbulences is an open question. This finding can be understood by considering species' growth rate, their sinking velocity, and their compensation depth. Small species have (i) a high *per capita* population growth rate, (ii) a relatively low sinking velocity, but (iii) a relatively shallow compensation depth (i.e., depth at which production from photosynthesis is equivalent to the costs). When turbulent diffusion is very low, individuals can stay in the light zone during a long period of time, which allows them to multiply before sinking. In other words, reproduction overcompensates for the sinking loss,

even if individuals are not naturally buoyant. This result is consistent with other studies demonstrating that small cells are able to remain at the surface of the water column due to medium viscosity (Pedrós-Alió *et al.*, 1989). The minimal level of turbulent diffusion allowing a small species to persist is very low: we found  $10^{-11}$  m<sup>2</sup>.s<sup>-1</sup> for a 1  $\mu$ m<sup>3</sup> cell using the classical formula given by Riley *et al.* (1949), which is far below the lowest diffusion rate measured in aquatic ecosystems (Daly & Smith, 1993). Hence, one can assume that small cells can persist in even the calmest water.

At the other end of the size spectrum, large species face inverted conditions (i.e., a relatively low *per capita* population growth rate and a relatively high sinking velocity). Therefore, in the absence of turbulence, individuals sink out of the euphotic zone too fast to allow growth to compensate for the sinking loss. These populations need turbulence to maintain individuals within the euphotic zone. Indeed, turbulence increases species motion in and out of the euphotic zone and their spread over the water column, and the strength of this process increases with turbulence strength. As a result, large cells are able to spend more time in the light zone at intermediate turbulence than at very low turbulence, which allows persistence of the population. Because growth decreases with body size, while sinking velocity increases with body size, a higher turbulent diffusion rate (i.e., a higher turbulence) is necessary to keep large cells within the euphotic zone. This is why the minimal strength of turbulence increases with body size.

However, if turbulence is too strong, individuals are mixed into the dark zone too fast and do not spend enough time in the light zone to allow the persistence of the population. This process operates on all species and explains the presence of an upper threshold of turbulence above which species cannot persist. High turbulence increases individual turnover between light and dark zones. Since large species have a low growth rate, these species need to spend more time in the light. However, since large species have a deeper compensation depth (i.e., a deeper light zone), they show an upper threshold at higher turbulence than smaller species. But, sinking velocity increases with size faster than compensation depth does. Therefore, for larger species, this upper threshold occurs between small and intermediate size species' thresholds. Nonetheless, it should be noticed that differences between species are quite small and might not have a strong impact in real ecosystems. Indeed, some field studies have shown that smaller phytoplankton species tend to dominate when turbulence is strong (Ward & Waniek, 2007), while other studies show that highly mixed systems tend to be dominated by large species (Kiørboe, 1993).

Another interesting result comes from the study of the depth profile given by the model. The model predicts that, at low turbulence, small species should have their maximal abundance at the surface, while species with large body size, provided they are able to survive, should reach their maximum abundance below the surface. Indeed, population growth is maximal at the surface, and this is where the majority of cells of the population accumulates, provided that reproducing cells get to stay sufficiently long in this zone. The accumulation of these cells close to the surface shades the light. Thus, growth becomes impossible below the surface. The depth of median population abundance (the depth where half of the population is located above and the other half below) is close to the surface (figure 2–3). The realized compensation depth is located close to the surface and above the species-specific compensation depth (i.e., the compensation depth in the absence of shade). However, when body size increases, sinking velocity becomes more and more important in the overall dynamic. This means that individuals are unable to stay close to the surface. Since fewer cells are located at the surface, light can reach deeper water. Thus growth is possible below the surface, and the depth of median population abundance is located below the surface (figure 2–3). For even larger cells, sinking velocity is too strong. The cells sink below their species-specific compensation depth and disappear. This pattern of maximum density below the surface observed for intermediate-size species is usually interpreted as a consequence of either nutrient limitation (Klausmeier & Litchman, 2001), photoinhibition (Worrest et al., 1978), or zooplankton grazing (Cullen *et al.*, 1992). Here, this pattern results only from the interplay between growth, shade, and sinking velocity (Huisman & Sommeijer, 2002b). Our model shows that this pattern can be explained by the interplay between gravity, body density, medium density, and light, without involving any other biological mechanism.

According to the model, phytoplankton cells larger than 10,000  $\mu$ m<sup>3</sup> cannot survive because they sink too fast at all turbulence levels. In real ecosystems, large phytoplankton cells usually increase their buoyancy by modifying their body density (Waite, 1992), so that even very large diatom species (e.g., *Ethmodiscus* species) can persist when turbulence is weak (Villareal, 1992). The abundances that our model predicts for small species (around  $10^8$  cells.mL<sup>-1</sup>) can be quite high. Although population growth is usually limited by several factors, the present study focuses on light limitation during bloom conditions, and nutrients are assumed to be non-limiting. However, once a phytoplankton bloom is beyond its peak, cells will have consumed the available nutrients, which in turn should become limiting, and population growth will sharply decrease (Boyd *et al.*, 2004; Elser *et al.*, 2007). As a consequence, real populations do not usually experience levels of abundance predicted by the model. Nonetheless, several empirical studies reported similar or even higher abundances (Agustí *et al.*, 1987; Miyazono *et al.*, 1992).

#### 2.5.2 Size-mediated relationship between depth and persistence

The model predicts that a critical depth is observed only at high turbulence for small species, while it is observed at both low and high turbulence for large species. Considering first, small species at low turbulence, their population is close to the surface. Below the surface, light availability is very low and does not allow growth. Any loss by sinking can easily be compensated by new growth. This phenomenon is independent of water column depth. Therefore, there is almost no critical depth for small species at low turbulence. However, at high turbulence, the population diffuses through the whole column. Hence, the population cannot persist for depths above Sverdrup's critical depth. This is why a critical depth is observed only at high turbulence for small species.

Considering now large-bodied species, at low turbulence, individuals sink too fast compared to their growth rate (see above). In a shallow system, light
availability is still high at the bottom, and, even if individuals sink fast, the population can thrive on the bottom. In this case, the maximal abundance is located at the bottom of the system, and even large species are able to persist in absence of turbulence. On the other hand, in a deep system, individuals sink into the dark zone before multiplying, and the population disappears. This is why a critical depth close to the compensation depth is observed at low turbulence. Considering now high turbulence, a Sverdrup's critical depth is observed for large as well as for smaller species. One can notice that the critical depth at high turbulence moves to deeper layers when body size increases, which is a consequence of the deeper light compensation depth of large-bodied species. Larger phytoplankton species are therefore expected to be able to grow in deeper systems than smaller species at high turbulence.

#### 2.5.3 Importance of body size on phytoplankton community structure

A major insight from this study is that effects of turbulence vary depending on both turbulence strength and species body size. The interplay between sinking velocity, body size and turbulent diffusion is the corner stone of population persistence. In the present study, size is considered as a master-trait for growth and sinking velocity, which provides a more realistic interplay between these two features of phytoplankton cells. The model assumes that species are denser than the surrounding medium, and therefore are prone to sinking. Hence, it appears that large-bodied species should not be able to thrive in calm water. Indeed, several species have specific adaptations that increase their buoyancy (e.g., gas vacuoles), which allows some larger species (such as *Microcystis, Anabaena*, Aphanizomenon, Trichodesmium or buoyant diatoms) to be abundant in relatively calm waters, while our results show that they should not persist in such conditions. According to our model, on the one hand, large species would benefit more than small species from an increase of buoyancy, because it would increase their optimal range of turbulence, especially toward low turbulence values. On the other hand, in deep and highly turbulent systems, all species would benefit from evolving traits that decrease turbulent diffusion because it would allow them to escape Sverdrup's critical depth constraint.

Our model assumes zero-flux boundary conditions at the top and the bottom, an assumption that was used in several other studies (Huisman & Sommeijer, 2002b; Huisman *et al.*, 2004; Ryabov & Blasius, 2014). However, other studies have used different boundary conditions or incompletely mixed systems (Huisman *et al.*, 1999a; Mellard *et al.*, 2011). Our model represents relatively shallow systems during spring mixing conditions and is best suited to study phytoplankton spring blooms that occur under such conditions. Boundary conditions under which cells are allowed to leave the system at the bottom of a thermocline are less realistic for this type of situation, and the combination of having a thermocline in a deep system with high turbulence may lead to the disappearance of all species from the system (Huisman & Sommeijer, 2002a).

Similarly it is known that shear stress from water mixing is another factor that potentially affects phytoplankton cells and can cause cell destruction, cell collision or agglomeration (Hondzo & Lyn, 1999). Because it is very difficult to quantify this shear stress and to define a clear relationship between this effect and cell size, we followed other studies (Shigesada & Okubo, 1981; Huisman & Sommeijer, 2002b; O'Brien *et al.*, 2003) and did not consider the effect of shear stress in our study.

All simulations were done using incident light intensity at  $3.5*10^{-4}$  mol photons.m<sup>-2</sup>.s<sup>-1</sup>, which is assumed to be a saturating condition at the surface. Robustness of the results has been tested using higher and lower light intensity. On the one hand, for higher irradiance, all species show a deeper compensation depth. Therefore, phytoplankton species are able to thrive deeper, which displaces the upper threshold of turbulence towards stronger turbulence values, while the lower threshold of turbulence occurs at lower turbulence. Furthermore, critical depth occurs deeper at high turbulence for all species. On the other hand, for lower irradiance, all species show a shallower compensation depth, which leads to an upper threshold of turbulence occurring at lower turbulence values, a lower threshold of turbulence occurring at higher turbulence, and a shallower critical depth. Overall, any change in incident light intensity creates quantitative but not qualitative changes in the results.

The present study provides new insight on phytoplankton bloom conditions. However, after the bloom period, other limiting factors (such as nutrients) will play an important role. Usually, nutrients are more abundant at the bottom of the system, while light is more available at the surface. Therefore, species requirement and uptake for nutrients and light create a trade-off that can lead to coexistence for some range of conditions (Huisman & Weissing, 1995; Diehl, 2002; Yoshiyama *et al.*, 2009). The population should be located close to the surface if light is more limiting, and deeper if nutrients are more limiting (Klausmeier & Litchman, 2001). Moreover, turbulence can also play a role by mixing cells as well as nutrients, therefore having an influence on species total biomass (Dutkiewicz *et al.*, 2009; Jäger *et al.*, 2010). A few studies considered interplay between light, nutrient and mixing, and their results are consistent with real observations (Valenti *et al.*, 2012; Denaro *et al.*, 2013; Valenti *et al.*, 2015).

Nutrients might also play another role because in our model, the *per capita* population growth rate is supposed to be a decreasing function of body size, in accordance with a number of empirical studies (Fenchel, 1974) and the metabolic theory of ecology (Brown *et al.*, 2004). However, this pattern can be altered by nutrient availability. Small species might be limited by nutrient uptake, as it is assumed to be an increasing function of body size, while large species might be limited by nutrient conversion into biomass, as it is assumed to be a decreasing function of body size. Therefore, the optimum for this trade-off should occur at intermediate size, leading to a unimodal relationship between growth and body size (Marañón *et al.*, 2013; Wirtz, 2013). This should have an effect on competition as species with an intermediate body size would be more productive than smaller species but deeper below the surface.

Nutrient limitation would also affect competition among phytoplankton species after the bloom period. Our model considers only one resource (light). According to the resource-ratio theory Grover (1997) as well as to niche theory (Chase & Leibold, 2003), competition between two species for only one resource should lead to the exclusion of the weaker competitor. Spatial segregation can sometimes allow species coexistence. In our model, a spatial segregation might transiently occur since a large-bodied species is able to thrive below the surface, and a smaller one thrives at the surface. However, as light comes from the surface, it means that the largest species tries to thrive in its competitor's shade, which is not sustainable (Huisman *et al.*, 1999a), unless nutrient limitation is included and traded off against light limitation.

Although a large number of studies considered the effect of nutrient limitation on phytoplankton competition (e.g., Ryabov & Blasius (2011, 2014); Kerimoglu *et al.* (2012)), considering size as a master-trait for light requirement, nutrient requirement, and sinking velocity over a wide range of body size remains challenging because species may have different trade-offs according to the nutrients considered (Litchman *et al.*, 2007). Nonetheless, we think that inclusion of nutrient limitation should be the next step to undertake.

Last, it should be noticed that the relationship between size and turbulence is not totally understood. Previous studies (Huisman *et al.*, 1999b; Huisman & Sommeijer, 2002b; Klausmeier & Litchman, 2001; Mellard *et al.*, 2011) considered (often implicitly) that the turbulent diffusion rate is the same for all species. Nonetheless, this assumption remains to be fully explored. Indeed, this might be a gross oversimplification given that the size and mass of phytoplankton species may differ by several orders of magnitude (e.g., a small cyanobacterium such as *Synechoccocus* has a volume of 18  $\mu$ m<sup>3</sup>, whereas a dinoflagellate such as *Ceratium hirundinella* has a volume of 44,000  $\mu$ m<sup>3</sup>). Mainstream theory (Kemp & Mitsch, 1979; Landahl & Mollo-Christensen, 1992; Ross & Sharples, 2008; Delhez & Deleersnijder, 2010) argues that because of their small size, phytoplankton cells live below the Kolmogorov scale. Therefore, cells are embedded within eddies and move with them, all at the same rate. However, studies on particle motion tend to demonstrate that particles diffuse more below Kolmogorov scale as their size decreases (Friedlander, 2000). Experiments demonstrated that planktonic cells show different response to shear according to their size Stocker & Stocker (2006). Last, some physical studies revealed the existence of sub-Kolmogorov scale velocity fluctuations (Zeff *et al.*, 2003; Schumacher, 2007). Hence, investigation of the relationship between size and turbulence should be an important step toward our understanding of phytoplankton community structure.

#### 2.6 Conclusion

Our study provides new insights into the conditions allowing algal blooms. It highlights that big and small phytoplankton species experience very different physical constraints in light-limited environments, potentially resulting in very different contributions to primary production depending on habitat depth and turbulence strength. In the future, the model may be extended to include nutrient limitation, which could allow the study of competition between phytoplankton and size-based food web dynamics.

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# 2.8 Appendices

# 2.8.1 Appendix A: Absorption cross-section

The absorption cross-section a is calculated as the following (Finkel *et al.*, 2004):

$$a = a^* c V_b \tag{A.2.13}$$

where  $a^*$  is the absorption surface per unit of chlorophyll a, and c is the chlorophyll a content *per cell*. This quantity is size-dependent (Finkel, 2001; Baird & Suthers, 2007).

$$c = 0.03 \ V_b^{0.69} \tag{A.2.14}$$

The absorption per unit of chlorophyll a includes the packaging effect, which also depends on body size (Morel & Bricaud, 1981)

$$a^{*} = \frac{3}{2} a_{s}^{*} \frac{Q_{\rho}}{\rho} \tag{A.2.15}$$

where  $a_s^*$  is the in vitro (unpackaged) absorption coefficient of chlorophyll a.  $Q_{\rho}$ and  $\rho$  are dimensionless numbers accounting for the packaging effect

$$Q_{\rho} = 1 + \frac{2e^{-\rho}}{\rho} + \frac{2e^{-\rho} - 1}{\rho^2}$$
(A.2.16)

$$\rho = a_s^* cd \tag{A.2.17}$$

where d is body diameter.

# 2.8.2 Appendix B: Sinking velocity

Sinking velocity is determined by three forces: weight, Archimedes' force, and drag.

$$F = gM_b - V_b\rho_m g - \frac{1}{2}S_b v^2 \rho_m C_d$$
 (B.2.17)

where g is the acceleration of gravity,  $\rho_m$  is the medium density, v is speed,  $S_b$  is the body section surface, and  $C_d$  is the drag coefficient. The drag coefficient ( $C_d$ ) is calculated according to an empirical rule (Turton & Levenspiel, 1986).

$$C_d = \left[0.352 + \left(0.124 + \frac{24}{Re}\right)^{0.5}\right]^2 \tag{B.2.18}$$

where Re is the Reynolds' number, which is calculated as the following:

$$Re = \frac{\rho_m v L_b}{\mu} \tag{B.2.19}$$

where  $L_b$  is body length, and  $\mu$  is the medium dynamic viscosity. Hence, considering Newton's second law, force divided by mass represents acceleration, which is the first derivative of speed by time.

$$\frac{dv}{dt} = g - \frac{V_b \rho_m g}{M_b} - \frac{1}{2} \frac{S_b v^2 \rho_m C_d}{M_b}$$
(B.2.19)

The sinking velocity is assumed to be an equilibrium speed, when all the three forces compensate each other (i.e., acceleration is null). Due to the recursive relationship between speed and drag, the sinking velocity at steady state is calculated by numerical approximation using the bisection method.

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Symbol	Meaning	Value	Units	References		
Variables:	<u></u>					
ω	Population abun-		$\mathrm{ind.m}^{-3}$			
	dance					
Ι	Light intensity		mol photons.m <sup><math>-2</math></sup> .s <sup><math>-1</math></sup>			
Physical p	arameters:					
g	Acceleration due to	9.81	$\mathrm{m.s}^{-2}$			
	gravity					
$ ho_m$	Medium density	1000	$kg.m^{-3}$			
$\mu$	Dynamic viscosity	0.00131	$ m N.s.m^{-2}$			
Re	Reynolds' number		dimensionless			
$C_d$	Drag coefficient		dimensionless			
$Z_{max}$	Water column depth		m			
$I_0$	Incident light inten-	$3.5 * 10^{-4}$	mol photons.m <sup><math>-2</math></sup> .s <sup><math>-1</math></sup>			
	sity					
$K_{bg}$	Background absorp-	0.2	$\mathrm{m}^{-1}$	Kirk (1994)		
	tion					
v	Advection (sinking		$\mathrm{m.s}^{-1}$			
	velocity)					
D	Diffusion (turbulent		$\mathrm{m}^2.\mathrm{s}^{-1}$			
	diffusion)					
Biological parameters:						
R	Reaction (per capita		$s^{-1}$			
<i>.</i>	net growth rate)		. 1			
$P(I_z)$	Gross photosynthetic		$mg C.s^{-1}$			
	rate at depth $z$		1			
$P_c$	Photosynthetic cost		$mg C.s^{-1}$			
$P_{max}$	Maximal gross photo-		$mol \ C.s^{-1}$			
	synthetic rate		1			
$k_{max}$	Maximal gross photo-	$7.75 * 10^{-18}$	$mol \ C.s^{-1}$	Reynolds $(1990)$		
	synthetic rate at ref-					
	erence size ( <i>Chlorella</i>					
	cell)	17	9			
$V_{0p}$	Volume at reference	$3.35 * 10^{-17}$	$\mathrm{m}^{3}$	Reynolds $(1990)$		
	size for photosyn-					
	thetic rate ( <i>Chlorella</i>					
	cell)					

Table 2–1: Parameters used in the model (part I)

Symbol	Meaning	Value	Units	References
a	Absorption cross-		$m^2$	
	section			
$a^*$	Absorption surface		$m^2.mg chla^{-1}$	
	per unit of chloro-			
	phyll a		0 1	
$a_s^*$	<i>in vitro</i> absorption coefficient	0.04	$m^2.mg chla^{-1}$	Finkel $et \ al.$ (2004)
$Q_{\rho}$ and $\rho$	Packaging effect		dimensionless	
c	Chlorophyll a content		${ m mg~chla.m}^{-3}$	
$C_0$	Carbon content at	$2.6 * 10^{-13}$	g C	Menden-Deuer
	reference size			& Lessard
			9	(2000)
$V_{0c}$	Volume at refer-	1	$\mu { m m}^{3}$	Menden-Deuer
	ence size for carbon			& Lessard
L	Content	0.1	-1	(2000)
$\phi$	photosynthesis	0.1	mol C. mol photon	Kirk (1994)
$\zeta$	Cost of photosyn-	$7*10^{-4}$	mol photon.mg $chla^{-1}$	Raven $(1984)$
	thetic apparatus			
au	Average lifetime	24	h	Riper <i>et al.</i>
	of photosynthetic			(1979)
	apparatus		- 1	
m	Metabolic loss		$J.s^{-1}$	
$l_d$	Death rate		ind.s <sup>-1</sup>	
$l_{0d}$	Death rate at refer-	$1.58 * 10^{-6}$	$S^{-1}$	McCoy &
<b>T</b> 7	ence size	1 00 103	3	Gillooly (2008)
$V_{0d}$	Volume at reference	$1.08 * 10^{\circ}$	$\mu { m m}^{ m o}$	MCCOY &
$\Gamma$	Size for death rate		Lind <sup>-1</sup>	Gillooly $(2008)$
	Dry ash free mass	0.16	J.III0 dimonsionless	
$I \iota_{dw}$	over wet mass ratio	0.10	umensiomess	
$E_{\perp}$	Energy over dry mass	23000	$k I k \sigma^{-1}$	
-dw	ratio	20000	no.ng	
$M_b$	Body mass (wet)		kg	
$V_b$	Body volume		$\mathrm{m}^{-3}$	
$S_b$	Body section surface		$\mathrm{m}^2$	
$L_b$	Body length		m	

Table 2–2: Parameters used in the model (part II)



Figure 2–1: Total abundance according to turbulent diffusion rate ( $Z_{max} = 60$  m). Small species are able to persist at very low turbulence strength, while bigger species need stronger turbulence for persistence. All populations disappear when turbulence is too strong. However, differences between species at high turbulence are quite small.



Figure 2–2: Depth profiles at steady state for three turbulent diffusion values. The left column represents a small species  $(1 \ \mu m^3)$  at respectively  $10^{-10}$  (A),  $10^{-6}$  (B) and  $10^{-3} \ m^2.s^{-1}$  (C). The right column represents a large species (650  $\ \mu m^3$ ) at respectively  $10^{-10}$  (D),  $10^{-8}$  (E) and  $10^{-5} \ m^2.s^{-1}$  (F). The small species maintains a population close to the surface at low turbulence. When turbulence increases, the population diffuses over the whole column. The large species maintains a population below the surface at low turbulence. When turbulence increases, the population has its maximum upwards. If turbulence increases more, the population spreads over the water column.



Figure 2–3: Median depth of the population at low turbulence according to cell size. When turbulent diffusion is very low  $(D = 10^{-10} \text{ m}^2.\text{s}^{-1})$ , the median depth of the population (solid line) of small cells is located close to the surface. Cells shade the light, and the realized compensation depth (dashed line) is located above the species-specific compensation depth (dashed-dotted line). Larger cells sink to fast and cannot maintain a population at the surface. Thus, the median depth of the population is at the bottom. For intermediate-sized cells (between the two vertical dotted lines), the median depth of the population is located below the surface. Since fewer cells are located close to the surface, light can reach deeper water, which allows cell growth below the surface, but above the species-specific compensation depth.



Figure 2–4: Water column depth  $(Z_{max})$  and turbulent diffusion interplay on algal bloom. For a small species  $(1 \ \mu m^3)$ , turbulence does not allow persistence beyond an upper threshold if the medium is too deep (A). On the other hand, a large species (1000  $\ \mu m^3$ ) cannot maintain a population if turbulence is either too low or too strong, and if the medium is too deep (B). The critical depth for the largest species is shallower at low turbulence strength.

# Connective statement # 2

In Chapter 2, I explored the effects of mechanical factors on primary producers. In Chapter 3, I explore the effects of these factors on consumers. Many studies emphasized patterns in food web structure. However, these patterns remain mostly empirical. Since, predation requires motion (by one way or another), mechanical factors should play an essential role in the ability for a predator to feed on a given prey. Hence, a predator needs to move to find a convenient prey, then it needs to capture this prey, and lastly it needs to maintain its prey during handling time. All these actions need energy related to motion, which is constrained by mechanical factors. The present chapter explores predator-prey interaction using a static model. It allows us to identify which predatory activities are the most limiting for a predator and which prey sizes a predator can feed on. This chapter also informs how predators have adapted to these constraints. The chapter considers aquatic and aerial systems, and a wide range of prey sizes. It gives new insights into how mechanical factors limit predator-prey relationships in these systems.

# Chapter 3

# The mechanics of predator-prey interactions: first principles of physics predict predator-prey size ratios

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**Portalier, Sébastien M. J.**<sup>1</sup>, Fussmann, Gregor F.<sup>1</sup>, Loreau, Michel<sup>2</sup>, Cherif, Mehdi<sup>3</sup>

<sup>&</sup>lt;sup>1</sup> Department of Biology, McGill University

 $<sup>^2</sup>$  Centre for Biodiversity Theory and Modelling, Station d'Ecologie Expérimentale du CNRS, 09200 Moulis, France

 $<sup>^3</sup>$  Department of Ecology and Envrionmental Science, Ume<br/>å University, SE-90187, Umeå, Sweden

#### 3.1 Abstract

Robust predictions of predator-prev interactions are fundamental for the understanding of food webs: their structure, dynamics, resilience to species loss, resistance to invasions and role in ecosystem functioning. Most current food web models are empirically based. Thus, they are very sensitive to the quality of the data, and ineffective in predicting emergent and disturbed food webs. There is a need for bottom-up, mechanistic models that predict the occurrence of a predator-prev interaction based on the traits of organisms and the properties of their environment. Here, we present such a model that focuses on the predation act itself. We built a Newtonian, mechanical model for the processes of searching, capture and handling of a prey item by a predator. Associated with general metabolic laws, we calculate the net energy gain from predation for pairs of predator and prey species of all given sizes. Interactions that result in positive net energy gains are deemed feasible and sustainable. Predicted interactions match well with data from the most extensive predator-prey database. Thus, our model shows that it is possible to accurately predict the structure of food webs using only a few ecomechanical traits. It underlines the importance of physics in structuring food webs.

**Keywords:** predator-prey interaction, trophic link, body size ratio, energy, mechanics, seach, capture, handling

#### 3.2 Introduction

Predicting predator-prey interactions accurately is fundamental. The dynamics of food webs depend critically on their structures (Allesina & Pascual, 2008; Allesina & Tang, 2012). Moreover, the fate of established and invasive species depends on the network of interactions in which they are embedded (Romanuk *et al.*, 2009). There is also increased awareness that ecosystem functioning itself depends critically on the structure of food webs (Thompson *et al.*, 2012). It is thus fundamental to understand what determines the occurrence of pairwise predator-prey interactions and by extension, the structure of food webs.

Most historical and contemporary models that predict the structure of food webs are empirically based. They derive rules from the regularities observed in well-studied food webs; devise statistical models that can reproduce these regularities in simulated food webs; and test the capacity of these statistical models to predict the structure of newly described food webs (Cohen & Newman, 1985; Solow & Beet, 1998; Williams & Martinez, 2000; Cattin et al., 2004; Eklöf et al., 2013; Gravel et al., 2013). While these models often succeed in faithfully replicating the patterns from which they are constructed, their performance worsens when it comes to other features of food webs (Allesina *et al.*, 2008; Williams & Martinez, 2008; Jonsson, 2014). Moreover, there are still limits to how accurate and detailed one can go in the description of food webs, despite steady improvements in the quality and quantity of food web data (Traugott *et al.*, 2013; Evans et al., 2016). As a result, most food web data are still irremediably spatially, temporally and/or taxonomically aggregated (Martinez et al., 1999; Berg & Bengtsson, 2007). Hence, statistical modeling approaches describe reasonably well food webs similar to those on which they have been built and trained, but

they might have issues to describe other food webs, knowing that discrepancies exist among ecosystems (Yvon-Durocher *et al.*, 2011).

Hence, a complementary "bottom-up" approach to food web modelling is thus needed, one in which pairwise interactions can be predicted from species traits and properties of the immediate environmental surroundings, the whole food web subsequently built by joining all the potential pairwise interactions between all species present (Stouffer, 2010; Petchey *et al.*, 2011).

One trait that has focused the attention of food web ecologists, and for good reasons, is body size (Cohen *et al.*, 1993; Emmerson & Raffaelli, 2004; Loeuille & Loreau, 2005; Petchey *et al.*, 2008; Gravel *et al.*, 2013). These studies have made great strides to reveal the role of size in structuring food webs, including its role in determining functional responses and interactions strengths (Brose, 2010; Thierry *et al.*, 2011). But here again, the patterns of prey-to-predator body size ratios and allometries used are empirical, thus they do not offer any mechanistic underpinning. Hence, the question of the factors that determine the size of the prey selected by a predator of a given body size remains incompletely understood as well as the mechanisms by which these factors operate.

To answer this question, we decided to adopt an analytical approach, concentrating on the core of predator-prey interactions, the act of predation itself, represented by the local search, capture and handling of one prey item by one given predator. The originality of our approach is to consider that this act of predation is by essence a mechanical interaction (fig. 3–1): the predator must set itself in motion to search and capture the prey, while the prey moves to avoid capture. The act of handling involves mechanical motion as well since the predator must maintain its position and standing in the water or air column while eating its prey. We used Newton's laws of mechanics associated with optimization techniques as a basis to estimate encounter rates, capture probabilities and handling times for all predator-prey pairs within a realistic range of body sizes. Combined with general laws about metabolic expenses in organisms, we then used this mechanical model to calculate an energy budget for the predator during this act of predation, and thus determine prey profitability. One advantage to our model is that only the body sizes of the species in the food web is used as input. No other parameter is fit from the data.

Thanks to the mechanical underpinning of our model, we can predict prey body sizes and profitability for both pelagic and flying predators. Including mechanics in ecological studies allows for unifying approaches and comparisons among systems rather than being restricted to a specific habitat (Webb, 2012). Hence, our model opens the door to a bottom-up prediction of the structure of food webs in diverse physical habitats, based only on a few mechanical traits of both predators and their prey.

#### 3.3 Methods

The model calculates a net energetic gain (G) for each predator to prey interaction

$$G = E - (C_s + C_c + C_h)$$
(3.1)

where E is energy received from the prey,  $C_s$ ,  $C_c$  and  $C_h$  are the costs for searching, capturing and handling the prey respectively. Most of parameters used in the model scale with body size  $(M_b)$ .  $M_{pred}$  refers to predator mass,  $M_{prey}$  refers to prey mass, and  $M_b$  refers to any body mass. The model is static and only includes energy allocations related to predation (i.e, no predator growth or reproduction).

## 3.3.1 Physical parameters

The model considers two different media (air and water). Parameters used by the model are acceleration due to gravity (g), body density  $(\rho_b)$ , medium density  $(\rho_m)$ , and medium dynamic viscosity ( $\mu$ , see table 3–1). Motion involves calculation of the drag coefficient in order to estimate speeds and related power outputs (see supplementary material 3.6.1).

#### 3.3.2 Biological parameters used by the model

These parameters are estimated using well-known allometric relationships (see supplementary material table 3–2). Real data points have been used to calibrate some parameters. These data points are different from those that were used to test the model predictions.

#### Energetic content

If the predator is able to find, capture and consume the prey, this predator will receive energy, which depends on the prey ash-free dry mass:

$$E = M_{prey} R_{dm} R_{ed} \tag{3.2}$$

Where  $R_{dm}$  is the ash-free dry mass to wet mass ratio, set as 0.16 (Ricciardi & Bourget, 1998), and  $R_{ed}$  is energy to ash-free dry mass ratio, set as  $23 \times 10^6$  J.kg<sup>-1</sup> (Salonen *et al.*, 1976).

#### Metabolic rate

Each predator has a metabolic expenditure *per time*  $(C_{met})$  that scales with body mass. To allow for energetic expenditure due to muscular effort, the field metabolic rate is used (Savage *et al.*, 2004; Hudson *et al.*, 2013):

$$C_{met} = 12.5 M_{pred}^{0.75} \tag{3.3}$$

Parameters were estimated from data (Hudson et al., 2013).

#### Maximal muscular output and stroke period

The maximal muscular output  $(F_{Max})$  that an organism can develop scales with body mass (Marden & Allen, 2002):

$$F_{Max} \le 55M_b \tag{3.4}$$

The time during which muscular forces are applied during motion, the stroke period, scales with body size:

$$t_{force} = 8 * 10^{-3} M_b^{0.25} \tag{3.5}$$

This parameter has been estimated from real observations of species-specific speeds (Dodson *et al.*, 1997; Leis & Carson-Ewart, 1997; Smayda, 2000; McDonald & Grünbaum, 2010).

#### **Detection distance**

A predator can detect a prey individual (and the prey can detect the predator) within its detection distance. A larger species should have a larger detection sphere. We used a simplified version of a previous model (Pawar et al., 2012)

$$D_{detec} = d_0 \left(\frac{M_b}{M_{0d}}\right)^{\frac{1}{3}} \tag{3.6}$$

where  $d_0$  is the detection distance at reference size (set at 0.225 m),  $M_{0d}$  is the reference mass (set at 0.0376 kg).  $d_0$  and  $M_0$  were estimated by regression from Pawar *et al.* (2012) (supplementary material).

#### 3.3.3 Framework for calculation of speed and work

Predation is broken down into three different processes (search, capture, handling) involving motion, which lead to three different costs (one for each process). Calculations of these three costs are all based on the same framework, where speed and cost are estimated using classical laws of Newtonian mechanic and fluid dynamics. However, the model assumes that species optimize different parameters for each predation process. Thus, the main framework of the calculation of speed and cost is presented first. Then, the specificities of each process are explained.

#### Rationale for calculation

Although animal motion is diverse, it is possible to define a common pattern. Animal motion can be represented as an oscillatory movement (Bejan & Marden, 2006), a pattern observed in swimming, running or flying animals. Thus, following this idea, we define a general framework for species motion.

Considering one oscillation, motion can be decomposed into a vertical and a horizontal component (fig. 3–2). Both are essential. The horizontal component represents the translational motion (i.e., the distance traveled between two points). However, this horizontal motion is impossible without a vertical motion that either lifts the body or the surrounding medium, allowing the horizontal movement (Bejan & Marden, 2006). The muscular output creates a force that is split between these two components.

# Vertical component

Vertical motion sequence during one oscillation includes four steps. During the first step, a muscular force  $(F_{Mv})$  is applied during the stroke period  $t_{force}$ . The body is lifted by this muscular force and Archimedes' force (due to medium density), but gravity and drag work in the opposite direction. The overall vertical force  $(F_v)$  writes as

$$F_{v} = F_{Mv} + g\rho_{m}V_{b} - gM_{b} - \frac{1}{2}vS_{b}\rho_{m}C_{d}$$
(3.7)

where v is instantaneous speed,  $S_b$  is the cross-section surface of the body, and  $C_d$ is the drag coefficient. According to Newton's second law, acceleration is equal to force divided by mass. It is also known that acceleration is the first derivative of speed with respect to time. Thus, instantaneous speed can be derived from equation 3.7:

$$\frac{dv}{dt} = \frac{F_{Mv}}{M_b} + \frac{g\rho_m V_b}{M_b} - g - \frac{1}{2} \frac{v S_b \rho_m C_d}{M_b}$$
(3.8)

During the second step, the muscular force stops (at time  $t_1 = t_{force}$ ), and the body pursues its lift by inertia until it stops (at time  $t_2$ ).

$$\frac{dv}{dt} = \frac{g\rho_m V_b}{M_b} - g - \frac{1}{2} \frac{v S_b \rho_m C_d}{M_b}$$
(3.9)

Third, the body falls (or sinks) passively back to its original vertical position (from time  $t_2$  to  $t_3$ ). During this sequence, motion is favored by gravity, but Archimedes'

force and drag work in opposition.

$$\frac{dv}{dt} = -\frac{g\rho_m V_b}{M_b} + g - \frac{1}{2} \frac{v S_b \rho_m C_d}{M_b}$$
(3.10)

At the end of one oscillation the body will end up at its original vertical position so that the animal stays at the same altitude or depth. The vertical component of the force thus sets the duration of the oscillation.

#### Horizontal component

The horizontal component includes two steps. During the first step, a muscular force  $(F_{Mh})$  allows a displacement of the body. This force is applied during the stroke period  $t_{force}$  (same as vertical component). For the horizontal component, since we do not pay attention to vertical forces, only drag matters.

$$\frac{dv}{dt} = \frac{F_{Mh}}{M_b} - \frac{1}{2} \frac{v S_b \rho_m C_d}{M_b} \tag{3.11}$$

During the second step, the force stops (at time  $t_1 = t_{force}$ ), and the body pursues its motion by inertia until its stops (from time  $t_1$  to  $t_3$  at the maximum).

$$\frac{dv}{dt} = -\frac{1}{2} \frac{v S_b \rho_m C_d}{M_b} \tag{3.12}$$

The total time  $(t_3)$  for both vertical and horizontal components is the same, as well as the duration of the active phase  $(t_{force})$ . It explains why the allocation of muscular force between the two components has a strong impact on the result because a total allocation to the vertical component is useless, since the individual stays at the same place (horizontally), while a total allocation to the horizontal
component is inefficient, since the individual cannot displace itself or the medium to move forward.

### Force allocation and work

Vertical  $(F_{Mv})$  and horizontal  $(F_{Mh})$  muscular forces are applied simultaneously during stroke  $(t_{force})$ . Thus, an animal can use up to its maximal muscular output for motion

$$0 < (F_{Mv} + F_{Mh}) \le F_{Max} \tag{3.13}$$

Due to the recursive relationship between speed and drag, equations 3.8 to 3.12 have to be solved numerically. Their integration through time gives the distance covered during one phase.

Then, knowing the forces  $(F_{Mv} + F_{Mh})$  applied during a period of time  $(t_{force})$ and the distance covered during that period of time in both vertical  $(x_v)$  and horizontal plan  $(x_h)$ , a work can be calculated, which is the energetic cost for motion.

Work = 
$$\int_{t_0}^{t_{force}} F_{Mv} x_v \, \mathrm{d}x + \int_{t_0}^{t_{force}} F_{Mh} x_h \, \mathrm{d}x$$
 (3.14)

This work can be divided by the time of a whole oscillation (from  $t_0$  to  $t_3$ ), thus having a cost *per time* (Cost<sub>pt</sub>).

$$\operatorname{Cost}_{pt} = \frac{\operatorname{Work}}{t_3 - t_0} \tag{3.15}$$

A last metric is used during the calculation of the costs: the total horizontal distance traveled  $(x_t)$ , which is the sum of the distance travel during active phase (from  $t_0$  to  $t_{force}$ ) and passive (inertial) phase (from  $t_{force}$  to  $t_3$ ).

#### Calculation of search, capture and handling costs

The three costs (i.e., searching, capture and handling costs) are calculated using the framework explained above. However, force allocation varies between the costs. For each cost, force allocation between the vertical and horizontal components are estimated using an optimization procedure based on the method of Simplex (Nelder & Mead, 1965).

## Searching cost

Searching cost represents energy spent by a predator to find its prey. It is based on a species-specific speed. This speed is assumed to be sustainable for a long period of time. Thus, it optimizes the horizontal distance traveled for a minimal cost.

$$(F_{Mv}, F_{Mh}) \Rightarrow \operatorname{Min}\left(\frac{\operatorname{Work}}{\overline{v}}\right)$$
 (3.16)

where  $\overline{v}$  is species-specific speed, which is the average speed throughout a whole oscillation.

$$\overline{v} = \frac{x_t}{t_3 - t_0} \tag{3.17}$$

Indeed, instantaneous speed is greater when the muscular force is applied, then it decreases. Thus, an average speed gives a fair estimate of a cyclic process. The optimization yields a species-specific speed that increases with body size. Species-specific speed is estimated for both predator and prey.

To be consistent throughout the whole study, prey is assumed to fill 1% of the total volume of the medium (White *et al.*, 2007). Therefore, small prey is more abundant than large prey. An encounter rate  $(E_r)$  is calculated (see supplementary material 3.6.2). Searching time is assumed to be the inverse of this encounter

rate. Searching cost is the sum of the mechanical cost and the metabolic cost (see above) during the search of a prey.

$$C_s = (\operatorname{Cost}_{pt} + C_{met}) \frac{1}{E_r}$$
(3.18)

## Capture cost

To keep it as simple as possible, a capture sequence is based on a unique oscillation: the predator jumps and tries to seize the prey. The prey jumps and tries to escape the predator. It is generalization based on the observation that many predators do not actually pursue their prey during a long period of time; predators usually try to capture the prey quickly, and if they fail, they stop (Weihs & Webb, 1984).

Motion during a capture sequence uses the framework described above. Now, the predator tries to optimize the distance  $(x_t)$  covered during a unique jump.

$$(F_v, F_h) \Rightarrow \operatorname{Max}(x_t)$$
 (3.19)

The predator may fail to capture the prey. Hence, a capture probability  $(P_{suc})$  is calculated. The prey can detect the predator if it is closer than the prey detection distance  $D_{prey}$  (see above). When the predator begins to jump, the distance between itself and its prey is assumed to be the prey detection distance ( $D_{prey}$ ). Duration of the jump  $(t_c)$ , distance covered  $(x_t)$  and speed (v) are calculated throughout the whole jump.

First, the predator must fill the distance  $(D_{prey})$  between itself and its prey before it stops (i.e., before v = 0), otherwise the probability of capture should be 0 ( $P_{suc} = 0$ ). Second, the relative speed between the predator ( $v_{Pred}$ ) and the prey ( $v_{Prey}$ ) at contact plays an essential role because if the prey is not able to move anymore, while the predator can pursue its motion, the probability of capture should be high. On the other hand, if the predator is at the end of its jump, while the prey can pursue its motion, the probability of capture should be low. We use a logistic function to describe this process:

$$P_{suc} = \frac{1}{1 + \frac{v_{Prey}}{v_{Pred}}} \tag{3.20}$$

We assume that if  $v_{Pred} = 0$ , it means that the predator is unable to fill the distance ( $P_{suc} = 0$ , as explained above).

The capture cost is paid by the predator no matter if the capture is successful or not. A low probability leads to multiple attempts before a success. This number of attempts is assumed to be the inverse of capture probability. The metabolic expenditure is paid for the duration of each jump  $(t_c)$ . Thus, the capture cost to effectively capture one prey is

$$C_c = (\text{Work} + C_{met} * t_c) \frac{1}{P_{suc}}$$
(3.21)

If  $P_{suc} = 0$ , this predator to prey interaction is not feasible.

## Handling cost

Handling cost represents the energy expenditure to maintain the prey during its consumption by the predator (i.e., during handling time). The mechanical handling cost is based on the idea that a predator living in the water or air column has to maintain prey body mass during handling time; otherwise this predator would lose its prey. Handling time depends on both predator and prey size (see supplementary material 3.6.3).

Using the framework explained above, the predator body moves downwards due to gravity, and energy is spent periodically to lift the body to its original altitude. The predator supports both its own mass and the prey mass. During the active period, the vertical component of the muscular force is applied. Therefore, the cost *per time* (equation 3.15) becomes

$$\operatorname{Cost}_{pt} = \frac{\int_0^{t_1} F_{Mv} x \, \mathrm{d}x}{t_3 - t_0} \tag{3.22}$$

Thus, handling cost is the sum of muscular and metabolic energy expenditure during handling time:

$$C_h = (\text{Cost}_{pt} + C_{met})t_h \tag{3.23}$$

If the predator cannot lift its body to its original altitude (or depth) while carrying the prey, it means that the predator is unable to carry this prey.

## 3.3.4 Size-related foraging costs and foraging limits

Each foraging cost (for searching, capturing, and handling the prey) varies with predator and prey sizes (supplementary material fig 3–6). The summation of these costs constrains feasible and sustainable interactions. Each cost constrains the range of prey that a predator can consume, defining foraging limits. These limits can be either energetic or mechanical.

## **Energetic limits**

Energetic limits occur when a prey does not provide enough energy compared to costs associated with its consumption. Limits are calculated for each foraging cost (search, capture and handling costs) separately.

$$G = E - C_s \tag{3.24}$$

$$G = E - C_c \tag{3.25}$$

$$G = E - C_h \tag{3.26}$$

where equation (3.24) determines the limit for search; equation (3.25) determines the limit for capture; equation (3.26) determines the limit for handling. A specific energetic limit can be defined by assuming that metabolism is the only cost.

$$G = E - (t_s + t_c + t_h)C_{met}$$
(3.27)

For each predator and for each cost, the smaller prey leading to G > 0 defines the corresponding energetic limit for this cost, which represents the minimal prey size that allows a given predator to fulfill its energetic expenditure for predation, when only the corresponding cost is considered. In other words, each energetic limit defines a lower size threshold for sustainable predator-prey relationships.

# Mechanical limits

Mechanical limits are related to capture and handling but are different from the energetic limits. Capture mechanical limit occurs when capture probability reaches 0, which means that the predator is unable to reach the prey, independent of the number of attempts. Similarly, handling mechanical limit occurs when the predator is unable to lift the prey during handling time. In both cases, the predator-prey interaction is assumed to be not feasible, and a gain is impossible to calculate. These limits occur because of a lack of sufficient muscular power for the predator.

#### 3.3.5 Use of empirical data

We compared model predictions with empirical data on predator-prey relationships (see supplementary material 3.6.4). Databases provided information on predator and prey body masses. For our analysis and presentation in graphs, data points were sorted and grouped according to whether or not interactions fitted the model's assumptions. These assumptions were that 1) the interaction occurs on a one-to-one base, 2) the predator tries to actively seize the prey, and the prey actively tries to escape the predator, and 3) both predator and prey can detect each other without interference (i.e., the predator cannot hide itself). Points that did not fit the model's assumptions were sorted according to which assumption was violated or relaxed. If several assumptions were violated, we considered the most limiting one.

We divided predators in our database in four groups. 1) Some predators fitted all the assumptions: those predators were pelagic or flying predators. 2) Some predators violated the capture assumptions. These predators feed on prey that do not move or move slowly compared to prey size, or these predators hunt in groups (i.e., not a one-to-one relationship). 3) Some predators violated the handling assumptions because they feed on more than one prey item at a time (i.e., microphagy). 4) Finally, some predators live or spend a large amount of time on the bottom (i.e., benthic predators, ground predators, or flying predators returning on the ground during handling time). These predators reduce handling cost by not carrying the prey, and they may take advantage of a complex landscape to hide themselves from the prey. They can come close to the prey before starting the capture sequence, thereby increasing the likelihood of a capture success.

# 3.4 Results

Combining a mechanical model of predation with metabolic laws allowed us to calculate the net gains in energy for a predator consuming a prey item of a given body size (see supplementary material fig. 3.6.4). Three cases can occur: (1) if an interaction leads to a positive net energetic gain, it is considered feasible and sustainable; (2) if the interaction leads to a negative net energetic gain, it is considered feasible but unsustainable; (3) if the predator cannot capture the prev, the interaction is considered unfeasible. We found that each predator can feed on a range of prey sizes that varies with its body size. Typically, larger predators feed on larger prey, as is often observed in nature (fig. 3–3). The model predicts that predators should be larger than their prey, and this constraint is stronger for flying than pelagic predators. The gains for predators of similar sizes are also consistently inferior for flying predators in comparison to pelagic ones. The prey giving the highest net energetic gain is always the largest prey that a predator can consume. Despite its simplifying assumptions, the model predicts most observed interactions from the most extent database of predator-prey body sizes currently published (Brose *et al.*, 2005), supplemented with data for flying predators that we collected directly from published articles. About 80% and 97% for pelagic and

flying predators, respectively ( $p < 10^{-5}$ , see supplementary material fig. 3–7), across the whole range of predator sizes (from zooplankton to large vertebrates).

In a second step, we analyze our model in detail to determine how do the different mechanical and energetic components of the model constrain the size of prey that a predator can consume. The maximum prey size that a predator can eat is determined by mechanical constraints. In effect, larger prey individuals can both detect a predator earlier and develop greater velocities (see Methods), resulting in successful escape. The result is that there is a maximum size for the prey that a predator of a given size can capture (solid blue lines on fig. 3–4). There is another mechanical constraint, which is related to handling. When the prey is too large, the predator is unable to develop sufficient mechanical power to hover while maintaining its prey in the water or air column (solid red lines on fig. 3–4). The lower of the two lines determines the maximum prey size for predators. With the set of parameters we chose, which are typical of generic, non-descript pelagic and airborne food webs (table 3–1 and supplementary table 3–2), it is capture that mechanically constrains the upper prey size (fig. 3–4).

We then look into the determinants of minimum prey size. Our model predicts that net energy gain limits minimum prey size. Energy given by a prey increases with its size (Supplementary figure S2). Hence, small prey sizes are poor energetic rewards for predators from the outset. There are four energetic costs that may further decrease small prey profitability: the searching cost, capture cost, handling cost, and metabolic cost. For small prey, each cost can by itself exceed the energy content of the prey. For predators larger than a few µg, handling cost is the largest cost, equaling the energy content of the prey (dashed red lines on fig. 3–4) for prey sizes that are well above the prey sizeswhere capture cost (dashed blue lines) and metabolic cost (dashed yellow lines) equal energetic content respectively. Handling cost is thus the most limiting cost for larger predators because the cost for hovering dominates over the other costs. For pelagic predators that are below the nanogram range (below the µg range for flying predators), searching cost is the limiting cost (green dashed lines on fig. 3–4). Small predators have short detection distances and low velocities resulting in too rare encounters under the prey densities assumed in the model (see Methods).

Not all predators in our dataset pay the full costs of searching, capturing and handling their prey.Some predators overcome the capture mechanical limit (red points on fig. 3–4) byfeeding on prey that do not move (e.g., on sponges or corals) or that move at a lower speed than expected according to their size (e.g., on gastropods). Such predators should be limited in their choice of prey by handling, the next process to act on the range of feasible prey sizes. Other predators decrease the cost of handling, which is mainly the cost of hovering in the case of small prey, by consuming several small prey items at a time, such as strikingly performed by plankton-feeding whales (blue points on fig. 3–4). Finally, a set of predators overcomes both the capture and handling limitations by living on the bottom (benthic, running or crawling predators; purple points on fig. 3–4). Such predators spend less energy on managing their buoyancy while handling their prey. Many flying predators, insects and birds, move to a hard surface during the handling of their prey, and thus belong to this category of predators. Since surfaces generally bear complex landscapes, predators can hide and come closer to their prey before being detected, which increases the likelihood of capture. Such predators have potentially no limits to the maximum size for the prey they can capture, in particular if they hunt in group. Our results however, show that this category of predators target prey with maximum prey sizes that are very close to the capture mechanical constraint (solid red lines on fig. 3–4).

## 3.5 Discussion

The present study presents a bottom-up, mechanistic and mechanical model that predicts occurrence of a predation interaction between a predator and a prey species with specified body sizes. For each predator size, we calculate the feasibility and energetic profitability from eating a prey of a given size, using a Newtonian, mechanical model associated with general metabolic laws. The size ranges of feasible and profitable predator interactions predicted compares well with observed interactions, as registered in the most extensive size-based predation database published so far (Brose *et al.*, 2005), augmented with additional data on flying predators.

There are a number of other mechanical models of food webs (Kondoh 2003; Loeuille Loreau 2005; Petchey et al. 2008; Maury Poggiale 2013; Carbone et al. 2014). Among these models, the allometric diet breadth model (ADBM) is the only model that, like our model, aims at predicting realized predation interactions, rather than at simulating non-descript, virtual food webs (Petchey *et al.*, 2008). ADBM adopts an approach that is similar to ours in many respects. Both models predict the diet of individual predator species based on body size as the main trait, and on a mechanistic model describing the energy gain from the prey. The choice of the mechanistic underpinnings is where the two models diverge: we base our calculations on a combination of mechanics and metabolic laws; ADBM is based on the optimal foraging theory (Beckerman *et al.*, 2006). Rather than confront the two models, we see them as complementary. ADBM uses empirical allometric relationships to include body size as a trait in the model, whose parameters need to be estimated from the food web datasets examined; we offer a mechanistic derivation of these allometries. ADBM does not subtract energetic costs from the energy content of the prey; we account for the costs related to the search, capture and handling of the prey. On the other hand, our model does not offer a ranking in the choice of prey, only net gain estimates; ADBM offer a clear ranking of species based on optimal foraging. Thus, we see the next obvious step in the development of our model in the combination of the two modeling approaches.

Our model matches some of the common body size patterns observed in food webs (Tucker & Rogers, 2014). Especially, predators consume smaller prey in air than water, but otherwise, the patterns remain similar. Thus, constraints due to mechanical factors are stronger in the air, but apply in the same way as in water. Another striking difference between the aquatic and terrestrial habitats is the greater number of predators that handle their prey in the water column, compared to the number of flying predators that handle their prey in the air (compare number of datapoints between the 2 panels of fig. 3–3). Our model provides an explanation: hovering costs are lower in the water column than in the air, due to higher buoyancy. Moreover, the bottom is generally farther from the pelagic predator position (in oceans and large lakes), requiring significant energy expenditure to be reached. In contrast, it is easier for flying predators to return to the ground (or any hard surface) during handling, to a degree that we could only find a few insectivorous bats and birds, as well as bat hawks, that matched the assumption of continuous hovering in the air (fig. 3–3b). More generally, since hovering is easier in water than in air, the predator motion during capture will have wider amplitude in water, which leads to a greater chance for the predator to reach its prey. It explains why, in air, predators are more constrained by the capture mechanical limit than aquatic predators.

Tucker & Rogers (2014) found another empirical pattern that can be explained by our model.Predator-prey body size ratiosare generally greater for carnivores than for herbivores. Usually, herbivores consume resources that do not move or move slowly compared to their size, so that they are able to overcome the mechanical limits set by the capture process. Carnivores face stronger mechanical capture limit because the prey can escape. Thus, a carnivore has better chances to capture a small prey than a large one, which leads to a larger body size ratio.In summary, our model offers a unique opportunity for a unified understanding of predator-prey patterns across habitats and trophic levels.

Despite the overall good performance of the model, we see that predators often preyon organisms that the model considers smaller than the optimal size. We think that this mainly from our use of generic, simplified allometric equations to describe important parameters in the model, such as prey population densities, maximum accelerations, and detection distances. Recent advances in the field of allometry have shown that the effect of body size can be more complicated than acknowledged (Pawar *et al.*, 2012; Wilson *et al.*, 2015; Hirt *et al.*, 2017a,b), although still predictable (Kiørboe & Hirst, 2014). Our model's predictability would certainly benefit from an increase in the realism of the allometric equations it uses.

There are other factors that may lead to a sub-optimum choice of prey in real ecosystems. The optimal prey might be absent, or show defense traits that make it challenging to find, capture or handle. Several studies have shown that further functional traits besides body size are necessary for an accurate prediction of trophic interactions (Wirtz, 2012; Eklöf *et al.*, 2013; Blanchard *et al.*, 2017). However, which traits need to be included first is yet debated (Boukal, 2014). Based on our model, and in accordance with other voices (Higham, 2007; Boukal, 2014), we propose as likely candidates the biomechanical traits related to predator and prey performances, after accounting for the effect of body size, i.e., deviations from allometries in velocities, accelerations and muscular forces.

There are also predators that feed on prey with body sizes beyond the predicted range of prey sizes. Such predators probably evolved strategies to get past the capture and handling mechanical limits. One important strategy is the ambush or sit-and-wait strategy (Kiørboe, 2011), which leads to the capture of larger prey than expected in terrestrial ecosystems (supplementary fig. 3–8).Our model suggests that the largest prey size for these predators is set by the handling mechanical limit (but not for web-weaving spiders). The lower prey size seems to be set by the energetic costs of capture for aquatic predators, and by the energetic

costs of handling for the terrestrial ones.Predators differ in other aspectsof their search (Bläßle & Tyson, 2016), capture (Higham, 2007) and handling strategies (Kiørboe, 2011). Building mechanical models with a similar approach to ours for most of the major predation strategies would certainly advance our understanding and predictability of food web structures.

Our model describes the interaction between a predator of a given size and a prey of a given size at a given moment in time, and it looks at the energetic balance between costs and gains during the predation act. But a predator usually needs to share its time between predation and other activities such as reproduction, recovery and the avoidance of its own predators. The energy gained from the predation act must also cover for these activities. Our model ignores these additional energetic costs for the time being and is thus anticonservative. The minimum prey size resulting in a positive net energy gain should be higher when all activities of the predator are included. It is far from obvious to calculate the energy cost related to the various activities of a predator. However, some existing allometric works open the door to such a development in our model (Hendriks & Mulder, 2008; Preisser & Orrock, 2012; Rizzuto *et al.*, 2017).

Despite the high level of abstraction of our model, we notice that it fits empirical data remarkably well. This suggests that predator-prey interactions in pelagic and aerial habitats are heavily constrained by mechanical factors despite hundreds of millions of years of evolution. It seems that numerous species follow the assumptions made by the model and stay within the limits imposed by mechanical and energetic constraints, while other species have adapted to overcome these limits in a way that is consistent with our model, albeit with relaxed assumptions (fig. 3–4). Overall, this suggests that physical factors have played a major role in the evolution of trophic interactions. Our model offers a general framework for the study of the mechanical bases of trophic interactions across a wide range of body sizes. It also provides general conclusions and mechanisms underpinning well-known empirical patterns in the structure of food webs beyond apparent discrepancies between media. Our work strongly emphasizes the need to consider the physical medium to understand the ecology of food webs (Denny, 2016). In that sense, it is an ecosystem approach at heart, one that does not separate the organisms "from their special environments, with which they form one physical system" (Tansley, 1935).

#### 3.6 Supplementary material

## 3.6.1 Drag Coefficient

For the calculation of motion, drag coefficient  $(C_d)$  is calculated using an empirical rule (Turton & Levenspiel, 1986) that offers a good approximation for very low as well as very high Reynolds numbers (see fig. S1).

$$C_d = \left[0.352 + \left(0.124 + \frac{24}{Re}\right)^{0.5}\right]^2 \tag{3.28}$$

where Re is the Reynolds number, which is calculated as the following:

$$Re = \frac{\rho_m v L_b}{\mu} \tag{3.29}$$

where v is speed, and  $L_b$  is body length.

## 3.6.2 Encounter rate

In order to be consistent throughout the whole study, prey is assumed to fill 1% of the total volume of the medium. Therefore, small prey is more abundant than large prey. Then, encounter rate  $(E_r)$  is calculated following Rothschild & Osborn (1988):

$$E_r = \frac{\pi \omega_{Prey} D_{pred}^2 (v_{Prey}^2 + 3v_{Pred}^2)}{3v_{Pred}} \quad \text{when } v_{Pred} > v_{Prey} \tag{3.30}$$

$$E_r = \frac{\pi \omega_{Prey} D_{pred}^2 (v_{Pred}^2 + 3v_{Prey}^2)}{3v_{Prey}} \quad \text{when } v_{Pred} < v_{Prey} \tag{3.31}$$

Where  $\omega_{Prey}$  is prey abundance,  $D_{pred}$  is the predator detection distance,  $v_{Pred}$  and  $v_{Prey}$  are the species-specific speeds for the predator and prey respectively.

#### 3.6.3 Handling time

Handling time is calculated as the sum of ingestion and digestion times. Ingestion time  $(I_t)$  can be described as the time needed for ingestion of a bite  $(B_t)$  times the number of bites needed to consume a whole prey.

$$I_t = B_t \frac{M_{prey}}{B_s} \tag{3.32}$$

where  $B_s$  is bite size, and  $M_{prey}$  is prey mass.

Bite diameter  $(B_d)$  depends on predator body mass (Wilson & Kerley, 2003)

$$B_d = B_0 \left(\frac{M_{pred}}{M_{0b}}\right)^{0.32} \tag{3.33}$$

Where  $M_{pred}$  is predator mass,  $B_0$  is bite size at reference size (set at 0.26 mm), and  $M_{0b}$  is reference size (set at 2.9 kg). Calibration has been done using published data Wilson & Kerley (2003). Assuming that a bite is generally spherical, the bite diameter can easily be transformed in a corresponding mass. Therefore, bite size  $(B_s)$  is

$$B_s = \rho_b \frac{4}{3}\pi \left(\frac{B_d}{2}\right)^3 \tag{3.34}$$

where  $\rho_b$  is body density.

Bite time  $(B_t)$  is the time needed to ingest a bite of size  $B_s$  (Laca *et al.*, 1994)

$$B_t = 0.1B_s^2 (3.35)$$

If the prey is smaller than the size of one bite (i.e.,  $M_{prey} < B_s$ ), bite time is assumed to be equal to the time for one bite (not a fraction of this time). Digestion time  $(D_t)$  depends on predator and prey body sizes (Hendriks, 1999)

$$D_t = D_{t0} \frac{M_{prey}}{B_s} M_{pred}^{0.25}$$
(3.36)

where  $D_{t0}$  is digestion time for 1 kg organism (set as  $2.3 * 10^4 \text{ s.kg}^{-1}$ ). Therefore, handling time  $(t_h)$  is

$$t_h = I_t + D_t \tag{3.37}$$

# 3.6.4 Empirical data

The following text is the metadata for the database used to test predictions from the model. Each entry in the database includes:

- Reference<sup>1</sup>
- Predator taxonomic name<sup>2</sup>
- Predator common name<sup>2</sup>
- Predator average mass  $(in kg)^3$
- Prey taxonomic name<sup>2</sup>
- Prey common name<sup>2</sup>
- Prey average mass (in kg)<sup>3</sup>
- Medium (either air or water)<sup>4</sup>
- Position (either column or bottom)<sup>5</sup>
- Statement on whether or not the described interaction fits the main assumptions of the model (i.e., either "Yes" or "No")<sup>6</sup>
- Which assumption is violated (or which violated assumption has the strongest effect)<sup>7</sup>

## Notes

<sup>1</sup> References link to studies where each entry was found (Barclay & Brigham, 1994; Barnes et al., 2008; Brose et al., 2005; Bull & Beckwith, 1993; Collins et al., 2010; Fuller, 1989; Gonsalves et al., 2013; Greenaway & Hutson, 1990; Hatton et al., 2015; Kaspari & Joern, 1993; Orlowski & Karg, 2013; Pithartova, 2007; Quinney & Ankney, 1985; Rakotoarivelo et al., 2007; Ross, 1964; Sierro et al., 2001; Todd et al., 1998). Some of these studies are meta-analysis; therefore the database does not necessarily refers to the original study where the data point was measured.

<sup>2</sup> Some studies provide only taxonomic or common species name. Missing information writes "NA".

<sup>3</sup> When another metric than body mass was provided (e.g., body volume or body length), it was converted into mass assuming an equivalent spherical shape.

<sup>4</sup> Medium refers to the medium where the interaction occurs, not the medium where either the predator or the prey may live. The full interaction has to occur within the same medium. Hence, species using interfaces between two media during their foraging activities where not considered.

<sup>5</sup> "Column" means that the predator spends the whole foraging activity swimming (for aquatic organisms) or flying (for aerial organisms) without taking a rest on a hard surface.

"Bottom" means that the predator spends most of its foraging time on a hard surface (either the bottom of an aquatic system, or the ground). <sup>6</sup> The main assumptions of the model are that 1) the interaction occurs on a one-to-one base, 2) the predator tries to actively seize the prey, and the prey actively tries to escape the predator, and 3) both predator and prey can detect each other without interference (i.e., the predator cannot hide itself). If an interaction fits these assumptions, then the present column shows a "Yes" statement, and the following column (violated assumptions) remains empty ("NA").

<sup>7</sup> If one (or several) assumption(s) was (were) violated, this column mentions the violated assumption (or the most important violated assumption).

"Hovering" means that the predator violates the hovering assumption, either because it lives on the bottom, or because it takes a rest during the most part of the feeding process.

"Capture" means that the predator violates the capture assumption, thus overcoming the capture mechanical limit: it may feed on prey that move slowly compared to their size, or it may hunt in group (i.e., not a one-to-one interaction).

"Microphagy" means that the predator consumes several prey at a time, thus overcoming the handling energetic limit: it violates the one-to-one relationship assumption.

"Ambush" means that the predator is an ambush (or sit-and-wait) predator. The case is not considered by the model since it involves a totally different mechanism, but it is discussed in the supplementary material.

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Symbol	Parameter	Value		Unit
		Water $10^{\circ}C$	Air $10^{\circ}C$	
g	acceleration due to gravity	9.81		$\mathrm{m.s}^{-2}$
$ ho_m$	medium density	1000	1.247	${\rm kg.m}^{-3}$
$\mu$	medium dynamic viscosity	$1.35 * 10^{-3}$	$1.768 * 10^{-5}$	$\rm N.s.m^{-2}$
$ ho_b$	body density	1080		${\rm kg.m}^{-3}$
Re	Reynolds number			dimensionless
$C_d$	drag coefficient			dimensionless

Table 3–1: Physical parameters



Figure 3–1: Main features of the model. The predator needs to spend energy to hover despite its weight (due to gravity), but it benefits from Archimedes' force. Predation is split into three sequences. First, the predator searches prey. Motion implies interplay between mechanical thrust, inertia and drag. Encounter is constrained by predator's detection distance ( $D_{detec}$ ), and prey abundance. A successful encounter leads to the second sequence: capture. During capture, the predator moves to seize the prey, while the prey tries to escape. In case of a successful capture, the predator needs to handle the prey during consumption and digestion times. During handling time, the predator needs to maintain hovering (lifting itself and the prey).



Figure 3–2: Framework for the calculation of motion cost. Motion is represented as an oscillation. An individual's body moves upwards, then downwards, while moving forward. Red arrows represent mechanical forces applied by the organism during the stroke period (from  $t_0$  to  $t_1$ ). Blue arrows are external forces due to the surrounding medium: Archimedes' force  $(\vec{A})$ , weight  $(\vec{W})$ , and drag  $(\vec{D})$ . Direction of arrows account for the component of motion they affect (horizontal or vertical component). A given oscillation is split into three phases: an active phase, where a mechanical force is applied by the body, then an inertial phase, where the body pursues its motion upwards until its stops, and last an inertial (descending) phase, where the body returns to its original vertical position. The overall horizontal distance traveled during this oscillation is the measured distance travelled by the organism (see Methods).



Figure 3–3: Net gains on predation for pelagic (A) and flying (B) predators. Heat maps show net energetic gains for predation on a one-to-one based interaction. Gains are weighed by predator mass (see methods) in order to allow comparisons between predators. When predator size increases, prey size should also increase because larger predators can capture larger prey. However, small prey do not provide enough energy, and therefore they become not sustainable for large predators. When predators feed on the largest prev that they are able to consume, net gains are similar despite differences in predator size. Points represent real interactions that fit the model assumptions within different aquatic systems either in marine or freshwater habitats, and for flying predators. In aquatic systems predator size of the empirical data ranges from rotifers to whales; 80% of the points fall within the predicted range of prey sizes. Freshwater and salt water did not show any significant difference. Thus, these ecosystems are shown together. In air, data are restricted to insectivorous bats and birds since many flying predators come back on the ground during handling time; 96% of the points fall within the predicted range of prey size.



Figure 3–4: Constraints on feeding interactions in aquatic (A) and terrestrial (B) systems. Dashed lines are the energetic constraints. They show the lower prey size allowing a positive net gain when the corresponding cost (search, capture, handling or metabolism) is the only cost acting on predation. Solid lines are the mechanical constraints (upper prey size that a predator can capture or handle under the model assumptions). Upper prey size is determined by capture mechanical constraint. Lower prey size is mostly constrained by handling energetic constraint. Lower predator size is determined by the successive addition of the four energetic costs, and by mechanical constraints. Colour of data points shows which constraint is relaxed. Red points are predators that overcome the mechanical capture constraint, thus being limited by handling mechanical and energetic constraints (red lines). Blue points are predators that overcome handling energetic constraint by consuming several small prey at a time. Purple points are predators living on a hard surface (bottom of aquatic systems or ground). They relax capture mechanical constraint since they can hide themselves, and they relax handling energetic constraint since they do not need to carry the prey, which explains the large spread of their diet breadth. These points include flying predators that return to the ground to handle their prey.

Table 3–2: Biological parameters (supplementary material)

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Symbol	Parameter	Value	Unit
$M_b$	body mass		kg
$V_b$	body volume		$\mathrm{m}^3$
$S_b$	cross-section surface of the body		$\mathrm{m}^2$
E	energy from the prey		J
$R_{dm}$	ash-free dry mass to wet mass ratio	0.16	dimensionless
$R_{ed}$	energy to ash-free dry mass ratio	$23*10^6$	$ m J.kg^{-1}$
$C_{met}$	metabolic rate		$\mathrm{J.s}^{-1}$
$D_{detec}$	detection distance		m
$d_0$	detection distance at reference size	0.225	m
$M_{0d}$	reference mass for detection distance	0.0376	kg
$B_d$	bite diameter		m
$B_s$	bite size		kg
$B_t$	bite time		S
$E_r$	encounter rate		$s^{-1}$
$P_{suc}$	capture probability		dimensionless
$I_t$	ingestion time		$\mathbf{S}$
$D_t$	digestion time		$\mathbf{S}$
$D_{t0}$	reference digestion time	$2.3 * 10^4$	$ m s.kg^{-1}$
$F_{max}$	maximal muscular output		Ν
$F_{Mv}$	vertical muscular force		Ν
$F_{Mh}$	horizontal muscular force		Ν
$t_{force}$	stroke period duration		$\mathbf{S}$
v	instantaneous speed		$\mathrm{m.s}^{-1}$
$x_t$	horizontal translational distance		m
$\operatorname{Cost}_{pt}$	cost (work) per time		$\mathrm{J.s}^{-1}$
$C_s$	searching cost		J
$C_c$	capture cost		J
$C_h$	handling cost		J


Figure 3–5: Drag coefficient as a function of Reynolds number (supplementary material). Drag coefficient decreases when Reynolds number increases as inertia becomes more important compared to viscosity. Thus, small animals, moving at low Reynolds number, face stronger drag compared to their size than larger animals, moving at higher Reynolds number.



Figure 3–6: Energetic gain and costs for each predator and prey interaction in pelagic systems (supplementary material). Energy given by the prey (A) increases with prey size. Searching cost (B) increases with prey size because predators need more energy to contact larger prey since prey abundance decreases with increasing prey size. This constraint is stronger for small predators because they move slowly, thus they spend more time to contact a large prey than larger predators would spend. Capture cost (C) increases mostly with predator size because a larger predator needs more energy to move. However, predators are unable to capture prey larger than an upper size threshold. This limit is stronger for small predators. Handling cost (D) increases mostly with predator size (for similar reasons than capture cost). Predators are unable to carry prey larger than an upper limit occurs at larger prey size than capture upper limit, which means that a predator overcoming this capture limit would be able to carry larger prey.



Figure 3–7: Permutation test for data points that fit the model assumptions for pelagic (A) and flying (B) predators (supplementary material). For each permutation, each predator was associated to a given prey size, randomly chosen with replacement from a uniform distribution (from minimal to maximal prey size of the database). Histogram shows distribution of number of points falling within the predicted area over  $10^5$  permutations. The red line shows the results from the original database. Flying predators show on average a better fit than pelagic predators because the range of sizes for both predators and prey is narrower. For both pelagic and flying predators, no permutation shows a result similar to or greater than the original database. Thus, the result is significant ( $p < 10^{-5}$ ).



Figure 3–8: Sit-and-wait predators in aquatic (A) and terrestrial systems (B) (supplementary material). These predators do not usually follow the main assumptions of the model. They do not move during searching time since they wait for a prey to come close to them. These predators usually live on the bottom, a complex landscape where they can hide, and where they can relax handling cost. Last, some might build traps (e.g., spider webs) that increase capture efficiency. Many sit-and-wait predators can consume prey larger than those predicted by the model. A full study of those predators is out of the scope of the present study.

### Connective statement # 3

I explored size-related effects of physical factors on primary producers in Chapter 2, and on consumers in Chapter 3. The model presented in Chapter 3 was a static model that explored feasible predator-prey interactions based on energetic net gains and mechanical limits. In the following chapter, a dynamic model of food web modules is used to explore effects of mechanical factors at the food web level. Equations from Chapters 2 and 3 are used to parameterize a dynamic model with primary producers (phytoplankton) and consumers. Producer-consumer interactions are explored analytically and numerically. Several food web modules are explored, across a wide range of body sizes. The model is based on explicit size constraints on predatory interactions. Thus, this chapter provides novel insights into food web structure since it leads to a better understanding of size ratios between predators and prey and size ranges of species that allow persistence of different modules.

## Chapter 4

# Effects of physical factors on the size structure of food web modules

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**Portalier, Sébastien M. J.**<sup>1</sup>, Cherif, Mehdi<sup>2</sup>, Fussmann, Gregor F.<sup>1</sup>, Loreau, Michel<sup>3</sup>

<sup>&</sup>lt;sup>1</sup> Department of Biology, McGill University

 $<sup>^2</sup>$  Department of Ecology and Envrionmental Science, Ume<br/>å University, SE-90187, Umeå, Sweden

 $<sup>^3</sup>$  Centre for Biodiversity Theory and Modelling, Station d'Ecologie Expérimentale du CNRS, 09200 Moulis, France

#### 4.1 Abstract

Trophic interactions are very common in natural systems. However, the structure of food webs is far from being fully understood. The physical components of the surrounding medium lead to mechanical constraints on species persistence and interactions. Focusing on some classical food web modules, we investigate how these constraints drive dynamics and persistence of these modules, and shape their size structure. The model shows that the dynamics of the system are mostly driven by predator size. Larger predators usually outcompete smaller ones, while smaller prey usually outcompete larger prey. The size ratio between intermediate consumers and phytoplankton is on average greater than the ratio between top predators and intermediate consumers. Both ratios are consistent with empirically observed interactions. Lastly, omnivorous top predators can persist only within a narrow range of sizes. This study provides new insights about size structure of food web modules.

**Keywords:** food web modules; mechanics; body size

#### 4.2 Introduction

Predator and prey interaction is a very common interspecific interaction, leading to a network of trophic interactions known as food webs. However, even though the study of trophic interactions began a long time ago (Lindeman, 1942), our understanding of the structure of food web remains incomplete and is still a challenge in ecology (May, 1999).

Studies on food webs usually focus on topology (Cohen *et al.*, 1990; Solow & Beet, 1998; Cattin *et al.*, 2004) and connectance using network approaches

(Stouffer *et al.*, 2006; Allesina *et al.*, 2008; Allesina & Pascual, 2009), but these studies either are descriptive or they predict patterns at community level using metrics measured at the community level, thus they ignore emerging properties coming from lower levels of organisation. Similarly, numerous studies investigated the stability of natural food webs compared to random food webs (May, 1973; Williams & Martinez, 2004; Rooney & McCann, 2012; Allesina *et al.*, 2015; Borrelli, 2015). Other studies investigate the role played by weak trophic links in the stability of the network (McCann *et al.*, 1998; Berlow, 1999; Neutel *et al.*, 2002; Emmerson & Yearsley, 2004; Gellner & McCann, 2016). All these studies provide very useful information, but the role played by the surrounding medium in constraining food web structure remains to be explored.

Living organisms are constrained by the physical properties of the surrounding medium (Denny, 1993, 2016; Vogel, 1988, 1996). Primary production relies on light availability, especially in aquatic systems. The interplay between weight and buoyancy is of primary importance for photosynthetic organisms to stay in the light zone (Shigesada & Okubo, 1981; Portalier *et al.*, 2016). Physical properties of the medium (such as gravity, density and viscosity) also affect consumers. Since predation usually implies motion, these factors create mechanical constraints acting on predators (Howland, 1974; Domenici, 2001; Domenici *et al.*, 2007, 2011). Previous studies usually focused on specific aspects of predation or on specific taxa, or investigated specific aspect of the medium such as dimensionality (Pawar *et al.*, 2012) or complexity (Barrios-O'Neill *et al.*, 2016). The present study investigates the role of the surrounding medium acting at the individual level on the structure of food web modules. Considering the link between the physical and the biological world would be a major improvement in our understanding of food web structure (Loreau, 2010).

The structure of a whole food web is complex, and it is shaped by numerous factors. These factors are often difficult to determine in practice. Hence, food web structure can show seasonality (Hagen & Auel, 2001; Acevedo-Trejos *et al.*, 2015; Leoni, 2017). Another issue comes from the resolution at which food webs are analyzed, leading to species aggregation (Solow & Beet, 1998; Arii *et al.*, 2007). Thus, the study of modules, which can be defined as subsets of food webs, may be a more convenient approach to study trophic dynamics and food web structure (Holt, 1977; Holt & Lawton, 1994). Food web modules have a simpler structure (Sauve *et al.*, 2016), thus they can easily be investigated, and can give insights into factors structuring food webs. Food web modules can be studied for their structure (Milo *et al.*, 2002) or their dynamics (Pimm & Lawton, 1977). Modules are present in all food webs (Pimm *et al.*, 1991). Many studies already focused on food web modules (Arim & Marquet, 2004; Bascompte & Melián, 2005; Gravel *et al.*, 2011) using different approaches, but most of them are descriptive. Thus, a mechanism explaining the structure and dynamics of food web modules is still pending.

Many existing mechanistic approaches focus on species traits (such as body size), thus using traits from lower levels of organization. Some of these studies use optimal foraging approaches (Křivan, 1996; Beckerman *et al.*, 2006; Petchey *et al.*, 2008). Nonetheless, they are usually restricted to a limited range of species. It appears that body size seems to be a good predictor of trophic position (Williams *et al.*, 2010) and plays a major role in structuring food webs (Cohen *et al.*, 1993). However, most of studies considering body size structure of food webs remain empirical (Gravel *et al.*, 2013; Barrios-O'Neill *et al.*, 2016). Thus, a more general approach using concrete traits (i.e., body size) and valid for a wide range of species would allow a better understanding of the size structure of food web modules.

The purpose of the present study is to investigate how constraints from physical factors affect the persistence and size structure of some classical food web modules. Thus, we propose a model that incorporates mechanical constraints related to body size on predation into a dynamic model of food web modules. Within the model, each species faces mechanical constraints related to its own size, while moving. These constraints narrow the range of prey size that a predator can feed on (Chapter 3), thus constraining species persistence and species coexistence through time. Other biological traits are related to size (such as metabolism, or photosynthetic rate for primary producers), thus species growth rate is also related to size. The model allows for investigating size structure of some species interactions (i.e., two to three species combinations) that lead to a sustainable interaction.

The real novelty of this approach is that it merges size-related biological and physical constraints within classical predator-prey systems. Most parameters in the model are related to predator and prey sizes. Therefore, it provides a better understanding of the size-structure of food web modules. Conclusions from the model are easily testable since the mechanisms are based on a size, which is a trait that is commonly and easily measured.

#### 4.3 Methods

The model describes predator and prey interacting within modules. the basal prey consists of photosynthetic organisms that do not move by themselves (phytoplankton). Predators consuming this prey can be viewed as zooplankton or any other phytoplankton feeder. Some modules include a top predator which is a predator feeding on a moving prey (the former consumer). In a first step, the food web module is a relatively simple one where a primary producer consumes light and is consumed by a predator. A full list of physical (table 4–1) and biological parameters for the prey (table 4–2) and the predator (table 4–3) is included in the present paper.

#### 4.3.1 Photosynthesis

Photosynthetic production is determined by a set of equations (see Portalier et al. (2016) for more details). The growth rate per capita (R) includes five different mechanisms. The first one is gross photosynthesis (P), which varies according to light availability (I), which itself varies with N. It describes the amount of energy gained by photosynthesis. However, photosynthesis has a cost, due to pigments synthesis, which is represented by the second term  $(C_p)$ . The following two terms are metabolic loss  $(C_m)$  and death rate  $(m_N)$ . The last term is loss by sedimentation over the water column of depth z. This loss depends on sinking velocity (v), which itself varies according to body size and physical factors (gravity, body density, medium density, medium viscosity).

$$R(N) = P(N) - C_p - C_m - m_N - \frac{v}{z}N$$
(4.1)

The photosynthesis rate (P), is a saturating function of the rate of photons captured by an organism (Finkel *et al.*, 2004)

$$P(N) = P_{max} \tanh\left(\frac{a\phi I}{P_{max}}\right) \tag{4.2}$$

where  $P_{max}$  is the maximal photosynthetic rate, a is the absorption cross-section, and  $\phi$  is the quantum yield of photosynthesis. Light is consumed by individuals, which leads to a competition for light. Thus, light availability (I) follows a Beer-Lambert's law (Huisman *et al.*, 2004), and therefore, varies with light absorption by populations within the water column.

$$I = I_0 \exp\left\{-aN\right\} \tag{4.3}$$

where  $I_0$  is the initial irradiance received on the top of the system (in mol photon.s<sup>-1</sup>), *a* is absorption cross-section (defined below). Thus, equation (4.2) writes

$$P(N) = P_{max} \tanh\left(\frac{a\phi I}{P_{max}}\right) = P_{max} \tanh\left(\frac{a\phi I_0 e^{-aN(t)}}{P_{max}}\right)$$
(4.4)

Both maximal photosynthetic rate  $(P_{max})$  and absorption cross-section (a) are scale with body size (Finkel & Irwin, 2000)

$$P_{max} = k_{max} \left(\frac{V_b}{V_{0p}}\right)^{0.75} \tag{4.5}$$

where  $k_{max}$  is the maximal photosynthetic rate at reference size,  $V_b$  is body volume, and  $V_{0p}$  is the volume at reference size: a *Chlorella* cell (Reynolds, 1990). The absorption cross-section (*a*) increases with body size (Finkel *et al.*, 2004) (see chapter 2 for details). The photosynthetic cost term  $(C_p)$  writes

$$C_p = \frac{cV_b\zeta\phi}{\tau} \tag{4.6}$$

where  $\zeta$  is the cost of photosynthetic apparatus,  $\tau$  is the average lifetime of this apparatus over which the cost of this apparatus is amortized,  $V_b$  is cell volume, and c is chlorophyll a content *per cell* (see appendix A for details on the calculation of chlorophyll content).

Photosynthetic rate (P) and photosynthetic cost  $(C_p)$  (in mol C.s<sup>-1</sup>) are both multiplied by the molar weight of carbon (12 g. mol C<sup>-1</sup>), and then divided by the amount of carbon  $(C_b)$  needed to produce one individual (Menden-Deuer & Lessard, 2000).

$$C_b = C_0 \left(\frac{V_b}{V_{0C}}\right)^{0.88} \tag{4.7}$$

where  $C_0$  is carbon content at reference size, and  $V_{0C}$  is volume at reference size.

Metabolic cost  $(C_m)$  scales with body size (Peters, 1986).

$$C_m = \frac{0.01 \ M_b^{0.75}}{E_N} \tag{4.8}$$

where  $E_N$  is energy content (i.e., the amount of energy within a given organism).

$$E_N = M_b R_{dw} E_{dw} \tag{4.9}$$

where  $M_b$  is body mass (wet mass),  $R_{dw}$  is the ratio between the dry ash-free mass and the wet mass, and  $E_{dw}$  is the ratio of energy to dry mass. Death rate is assumed to be inverse of the lifespan, which is itself sizedependent (Peters, 1986)

$$m_N = m_0 * \left(\frac{M_b R_{mw}}{M_{0m}}\right)^{-0.22}$$
 (4.10)

where  $m_0$  is death rate at reference size, and  $M_{0m}$  is reference size.

Sinking velocity evaluates the relative importance of an organism's weight and buoyancy. A sinking force (F) is calculated, including as its terms three forces that act constantly on organisms. The first term is weight (i.e., the effect of gravity on the body) and is oriented downwards. The second term represents buoyancy (i.e., Archimedes' force) and is oriented upwards. The last term represents drag (i.e., the effect of medium viscosity and density) and is always opposed to motion. This model considers only one component of drag, which is surface drag.

$$F = gM_b - V_b\rho_m g - \frac{1}{2}S_b v^2 \rho_m C_d$$
(4.11)

where  $M_b$  is body mass,  $V_b$  is body volume,  $S_b$  is body cross-section surface, gis acceleration due to gravity, v is sinking velocity,  $\rho_m$  is medium density, and  $C_d$  is drag coefficient (see appendix B for details about drag coefficient and sinking velocity). Hence, considering Newton's second law, force divided by mass represents acceleration, which is the first derivative of speed by time.

$$\frac{dv}{dt} = g - \frac{V_b \rho_m g}{M_b} - \frac{1}{2} \frac{S_b v^2 \rho_m C_d}{M_b}$$
(4.12)

The sinking velocity is assumed to be an equilibrium speed, when all the three forces compensate each other (i.e., acceleration is null). Due to the recursive relationship between speed and drag, the sinking velocity at steady state is calculated by numerical approximation using the bisection method.

Overall, R(N) represents a net *per capita* growth rate. This net *per capita* growth of photosynthetic organisms decreases when body size increases. The overall *per capita* growth rate calculated is in accordance with empirical observations (Finkel *et al.*, 2010).

#### 4.3.2 Predation

A predator receives energy from its prey, but it first needs to search, capture and handle this prey. Each predation process leads to time and energetic expenditures. Thus, predation on a given prey requires time for searching  $(t_s)$ , time for capturing  $(t_c)$  and time for handling  $(t_h)$  this prey, and the predator has to pay associated energetic costs for searching  $(C_s)$ , capturing  $(C_c)$  and handling the prey  $(C_h)$ . Each predatory activity implies motion, and motion is constrained by physical factors (gravity, medium density and medium viscosity). Motion is represented as an oscillatory process (Bejan & Marden, 2006). A full description of the calculation of predation parameters can be found in Chapter 3. Only the main features playing a role in the functional response and conversion coefficient are mentioned here.

During searching time, both predator and prey move at a species-specific speed ( $v_P$  for predator and  $v_N$  for prey) that scales with body size. A given predator will encounter an individual from the prey population at a rate ( $E_r$ ) (Rothschild & Osborn, 1988) depending on prey abundance (N), and predator detection distance  $(D_P)$ .

$$E_r = \frac{\pi N D_P^2 (v_N^2 + 3v_P^2)}{3v_P}$$
(4.13)

In case of a phytoplankton cell (primary producer), the prey is assumed not to move ( $v_N = 0$ ). For a given predator species and a given prey species, all parameters are constant except prey abundance (N). Thus, encounter rate can write

$$E_r = \frac{\pi D_P^2 (v_N^2 + 3v_P^2)}{3v_P} N = \beta N$$
(4.14)

Once a prey is detected, the capture sequence begins. The predator jumps and tries to seize its prey, while the prey tries to escape, the distance between the predator and the prey is assumed to be the detection distance of the prey. Relative speed at time when predator reaches the prey leads to a capture probability  $(P_c)$ .

$$P_c = \frac{1}{1 + \frac{v_N}{v_P}}$$
(4.15)

If the predator cannot reach the prey, then  $P_c = 0$ . When the prey is a phytoplankton organism, capture is assumed to always be successful ( $P_c = 1$ ).

Searching time is assumed to be the inverse of encounter rate times the probability of capture (i.e., the time needed to contact one prey that would lead to a successful capture).

$$t_s = \frac{1}{E_r P_c} \tag{4.16}$$

Capture time  $(t_c)$  is the time needed for the predator to reach the prey during that jump.

Last, the predator has to maintain itself and the prey in the water column during handling time. Handling time  $(t_h)$  is the time needed to consume the prey.

$$t_h = B_t \frac{M_N}{B_s} \tag{4.17}$$

where  $B_t$  is bite time,  $B_s$  is bite size,  $M_N$  is prey mass. Bite size scales with predator size (Wilson & Kerley, 2003)

$$B_{s} = \rho_{b} \frac{4}{3} \pi \left( \frac{B_{0}}{2} \left( \frac{M_{P}}{M_{0b}} \right)^{0.32} \right)^{3}$$
(4.18)

where  $B_0$  is bite diameter at reference size,  $M_{0b}$  is reference size, and  $\rho_b$  is body density. Bite time depends on bite size (Laca *et al.*, 1994)

$$B_t = 0.1B_s^2 \tag{4.19}$$

#### 4.3.3 Functional response

The functional response is defined as the inverse of the time needed for searching, capturing and handling one unit of prey.

$$f(N) = \frac{1}{\frac{1}{E_r * P_c} + t_c + t_h} = \frac{1}{\frac{1}{N\beta P_c} + t_c + t_h} = \frac{N\beta P_c}{1 + N\beta P_c(t_c + t_h)}$$
(4.20)

Given the assumptions made on the encounter rate, it is a type II functional response.

#### **Conversion efficiency**

Conversion efficiency represents the amount of predator biomass produced by consumption of a given prey biomass. A predator receives an energetic net gain (G) for each prey.

$$e = \frac{G}{E_p} \tag{4.21}$$

where  $E_p$  is energy content for a given predator. The net gain represents energy received from the prey  $(E_N)$  minus the costs associated by predation of that prey: costs for searching  $(C_s)$ , capturing  $(C_c)$ , and handling  $(C_h)$  that prey.

$$G = E_N - (C_s + C_c + C_h) \tag{4.22}$$

 $E_N$  and  $E_p$  are calculated in the same way (see equation 4.9).

Each cost implies motion, and motion is constrained by physical factors (gravity, medium density and medium viscosity). See chapter 3 for detailed explanations. Searching cost is the product of mechanical cost for motion at species-specific speed ( $C_{spt}$ ) and metabolic cost *per time* ( $C_m$ ) by searching time ( $t_s$ ).

$$C_s = (C_{spt} + C_m)t_s \tag{4.23}$$

During capture sequence, energetic cost (mechanical cost and metabolic cost) for reaching the prey is paid even if the predator fails to capture the prey. Thus, the cost for a successful capture writes

$$C_c = Cost * \frac{1}{P_c} \tag{4.24}$$

If the predator cannot reach the prey  $(P_c = 0)$ , then the interaction is assumed to be not feasible.

Last, the predator has to maintain itself and the prey in the water column during handling time  $(t_h)$ . Energy expenditure during handling time is the sum of mechanical  $(C_{hpt})$  and metabolic loss per time.

$$C_h = (C_{hpt} + C_m)t_h \tag{4.25}$$

Since the cost for searching a prey depends on prey abundance (see equation 4.13), conversion coefficient varies with prey abundance. Thus, it writes e(N).

#### Food web modules

First, the model investigates a simple one predator - one prey system.

$$\frac{dN}{dt} = R(N) - f(N)P$$

$$\frac{dP}{dt} = e(N)f(N)P - m_pP$$
(4.26)

where N is the photosynthetic prey (i.e., primary producer), P is the consumer, and R(N) is growth rate of photosynthetic rate. Predator death rate  $(m_p)$  is calculated in the same way as prey death rate (see equation 4.10). Predator size ranges from 1 ng, which is below the minimal predator size that should persist (see chapter 2), up to 10<sup>6</sup> kg, which is a very large size. Hence, simulations should cover the majority of existing predators. Prey size ranges from 1 pg, which corresponds roughly to a 1  $\mu$ m<sup>3</sup> phytoplankton cell, up to 0.35  $\mu$ g (about 30,000  $\mu$ m<sup>3</sup>), which is the maximal size that a phytoplankton cell can persist according to the model, when there is no predation. Combinations of predator and prey sizes were chosen regularly within these ranges.

Next, the model investigates a two prey - one predator system. The two species of prey compete for light and are hunted by the same predator. This module represents the so-called "diamond shape" system that is a common module within real food webs. Only predator and prey sizes that lead to persistence of the consumer in a one predator - one prey system were kept for this system and the following ones.

$$\frac{dN_1}{dt} = R_1(I) - f_1(N_1)P$$

$$\frac{dN_2}{dt} = R_2(I) - f_2(N_2)P$$

$$\frac{dP}{dt} = e_1(N_1)f_1(N_1)P + e_2(N_2)f_2(N_2)P - m_pP$$
(4.27)

A third module investigated is a two predators - one prey system.

$$\frac{dN}{dt} = R(I) - f_1(N)P_1 - f_2(N)P_2$$

$$\frac{dP_1}{dt} = e_1(N)f_1(N)P_1 - m_{p1}P_1$$

$$\frac{dP_2}{dt} = e_2(N)f_2(N)P_2 - m_{p2}P_2$$
(4.28)

A more complex system, a food chain, is then studied: one species is a photosynthetic species that is consumed by a phytoplankton feeder, and a toppredator consumes the former consumer. Size range of the top predator is similar to the initial size range of the intermediate consumer (for the one predator - one prey system).

$$\frac{dN}{dt} = R(I) - f_1(N)P_1$$

$$\frac{dP_1}{dt} = e_1(N)f_1(N)P_1 - f_2(P_1)P_2 - m_{p1}P_1$$

$$\frac{dP_2}{dt} = e_2(P_1)f_2(P_1)P_2 - m_{p2}P_2$$
(4.29)

where N is the photosynthetic prey (i.e., primary producer),  $P_1$  is the intermediate predator, and  $P_2$  is the top-predator. An even more complex system is investigated, where the top-predator is omnivorous. The same size range was used.

$$\frac{dN}{dt} = R(I) - f_1(N)P_1 - f_2(N)P_2$$

$$\frac{dP_1}{dt} = e_1(N)f_1(N)P_1 - f_2(P_1)P_2 - m_{p1}P_1$$

$$\frac{dP_2}{dt} = e_2(N)f_2(N)P_2 + e_2(P_1)f_2(P_1)P_2 - m_{p2}P_2$$
(4.30)

Systems are solved numerically. However, an analytical exploration of the one predator - one prey system is presented in order to describe the main features of the predator to prey dynamics of the model.

#### 4.3.4 Statistical analysis

Size distributions of predators were compared between the different outcomes of the one predator - two prey modules. Size distributions between predators and between prey were tested using Kruskal-Wallis test and Mann-Whitney post-hoc test with Bonferroni correction, since data were non-normally distributed.

#### 4.3.5 Empirical data

Predicted body size ratios for phytoplankton feeders (one predator - one prey systems) and top predators (food chains) are compared with observed body size ratios. Data points for predators feeding on phytoplankton are selected entries from the database provided by Brose *et al.* (2005). Data points for top predators come from the database used in Chapter 3 for pelagic predators. Points were selected if they met the model's assumptions: it is a one-to-one interaction (one predator feeds on one prey at a time), and the predator stays within the water column during the whole interaction time (i.e., search, capture, and handling).

#### 4.4 Results

The first food web structure explored is a simple two-species food chain, where a photosynthetic organism (i.e., the primary producer) is consumed by a predator. Since prey growth depends on light availability, prey population reaches a carrying capacity in the absence of predator. This carrying capacity is size-dependent (i.e., smaller prey will reach a greater abundance than larger prey). Moreover, light is the only basal resource. Thus, if several primary producers compete for light, the smaller species is always the best competitor.

#### 4.4.1 One predator - one prey system: analytical exploration

The functional response (equation 4.20) is of type II. It appears that when prey size increases, a predator will become saturated more quickly. Moreover, the maximal consumption rate will be lower as prey size increases (see fig 4-1). Equation (4.26) can be fully developed and writes

$$\frac{dN}{dt} = P_{max} \tanh\left(\frac{I_0 e^{-aN} a\phi}{P_{max}}\right) \frac{12}{C_{carb}} N - (C_p + C_m + m_n) N - \frac{v}{z} N - \frac{N\beta P_c}{1 + N\beta P_c (t_c + t_h)} P_{carb}$$
(4.31)

for the prey and

$$\frac{dP}{dt} = \frac{E_n - (\frac{1}{N\beta}C_s + C_c + C_h)}{E_p} \frac{N\beta P_c}{1 + N\beta P_c(t_c + t_h)} P - m_p P$$
(4.32)

for the predator.

Prey Zero Net Growth Isocline (ZNGI) can be determined by setting equation (4.31) to 0 and rearranging.

$$\overline{P} = \left(\frac{1}{\beta P_c} + N(t_c + t_h)\right) \left(P_{max} \tanh\left(\frac{I_0 e^{-aN} a\phi}{P_{max}}\right) \frac{12}{C_{carb}} - (C_p + C_m + m_n) - \frac{v}{z}\right)$$
(4.33)

The first bracket refers to predation parameters (search, capture, and handling), while the second bracket refers to prey overall growth rate. The isocline is humpshaped as expected for a type II functional response. For a given prey, when predator size increases, encounter rate increases at a higher rate than other predatory parameters. Therefore, all elements within the first bracket of equation (4.33) decrease, which leads to a shift of prey isocline towards lower values of  $\overline{P}$ (see fig 4–2-B). It means that the prey becomes limited by the predator at lower predator abundances. When prey size increases, the maximal *per capita* growth rate decreases, while sinking velocity increases. Thus, the maximal population abundance decreases, which leads to a shift of the curve towards lower prey abundance (see fig 4–2-A). The fact that the predator becomes saturated more quickly when prey size increases (see above) leads to a shift of the peak towards lower prey abundances.

The predator ZNGI can be determined by setting equation (4.32) to 0 and rearranging.

$$\overline{N} = \frac{m_p E_p + E_n P_c C_s}{\beta P_c (E_n - (C_c + C_h) - m_p E_p (t_c + t_h))}$$
(4.34)

The overall isocline is a straight line, since the result is constant for a given predator feeding on a given prey. For a given predator size, when prey size increases, energy given by the prey increases and the denominator increases faster than the numerator. Thus, the isocline is shifted towards lower prey abundances, which means that the predator needs a smaller amount of large prey than small prey to sustain a stable population (see fig 4–2-C). For a given prey, when predator size increases, encounter rate ( $\beta$ ) increases, as well as costs associated with predation and predator's requirements ( $E_p$ ). Hence, the denominator first increases (as  $\beta$  increases), which leads to a shift of the isocline towards lower prey abundances. Then, the increase of costs and requirements becomes dominant over encounter rate, and the denominator decreases, which leads to a shift of the isocline towards higher prey abundances (see fig 4–2-D).

Dynamics were determined by considering the relative position of the crossing point of predator and prey ZNGIs and the peak of the prey isocline. If ZNGIs cross on the left part of the curve (left to the peak), the resulting dynamic are persisting oscillations, while cases where ZNGIs cross on the right lead to a stable fixed point equilibrium. The dynamics are mostly driven by predator size (see fig 4–3). For small predators, interactions lead to a stable point equilibrium. When predator size increases, it leads to persisting oscillatory dynamics: predator and prey populations oscillate between a minimum and a maximum value. Considering a given prey size, a change in predator size does not significantly change the position of the peak for the prey ZNGI (fig 4–2-B), while it strongly affects the position of the predator ZNGI (fig 4–2-D). Thus, when predator size increases, predator ZNGI moves from the right to the left side of the peak, which leads to a switch of dynamics from a single point equilibrium to persisting oscillations. Even if this isocline can move back for large predators (fig 4–2-D), it does not go beyond the peak; thus conditions at steady state do not change. Nonetheless, prey size also plays a role since the relationship between predator and prey sizes determines feasible interactions (see below).

#### 4.4.2 One predator - one prey system: numerical exploration

Analytical and numerical analysis are concordant. There is a range of predator-prey sizes that allows for persistence of both the predator and the prey. Above a given size, a prey does not persist on its own (and therefore, a predator does not persist either). Another situation arises when the predator is unable to handle the prey. Such an interaction is assumed to be not feasible.

The shape of the persisting range of predator-prey sizes shows that both very small and very large predators feed on large prey, while intermediate size predators use a wider range of prey sizes (fig 4–3-A). Initially, very small consumers within the chosen size range cannot have positive population growth because they are limited by mechanical and energetic costs (see *chapter 2*). Larger consumers can achieve positive growth, but above a given size, energy intake through

phytoplankton cannot compensate for mortality anymore. Energy requirements increase with consumer size. A larger consumer needs to increase energy intake rate, which means that it should either capture more prey or capture larger prey. Since phytoplankton size is bounded, above a given size, large consumers can only increase capture rate, which also reaches an upper limit. Thus, when the phytoplankton species is too small compared to consumer size, it fails to provide a sufficient amount of energy to this consumer at a satisfactory rate. These interactions are not sustainable for a consumer population, which constrain the parameter space (fig 4–4).

Surprisingly, small predators can persist when large prey is present. This can be explained by the fact that, for a small predator, the successful capture of a large prey gives a large amount of energy compared to predator requirements. For example, considering only gross amount of energy given by the prey, consumption of a large prey item by a large predator represents  $10^{-5}\%$  of its needs. The same prey consumed by a small predator represents more than 50% of its needs. Moreover, the phytoplankton prey does not move, which means that small predators do not face any capture issues.

The body size ratio between predator and prey (fig 4–5) is consistent with real data (Brose *et al.*, 2005).

#### 4.4.3 One predator - two prey system

Most species interactions lead to competitive exclusion of one prey species. It is usually the larger prey species that is excluded (blue boxes on fig 4–6). But, when the predator is much bigger than the prey, the larger prey species can persist, while the smaller prey species is excluded. Some interactions lead to coexistence of both prey species. There is no significant different between predator sizes that drive either the smaller or the larger prey to extinction 4–7), while predators allowing coexistence between both prey are significantly smaller than predators from the two former groups (p-value  $< 2.2 \times 10^{-16}$ ). An equivalent patten does not appear clearly for prey size.

Prey size distribution shows that larger prey species are usually outcompeted by smaller prey species (fig 4–7-B), except when both prey species are very small (in this rare case, the larger prey outcompetes the smaller one). If one compares *per capita* growth rate of phytoplankton organisms (equation 4.1), a smaller organism has a higher photosynthetic gross production (see equation 4.5) and a lower sinking velocity. Thus, in the absence of predator, the smaller competitor outcompetes the larger one because it decreases available light below the minimum light requirement of the larger competitor. The presence of the predator can decrease competition pressure over the larger phytoplankton organism and may allow coexistence. This coexistence occurs when both prey are relatively small compared to cases where the larger prey is excluded (fig 4–7-B). Hence, the smaller prey is consumed but not driven to extinction by the predator, while the larger prey is not extirpated (either by overconsumption or competitive exclusion).

#### 4.4.4 Two predators - one prey system

Interactions usually lead to competitive exclusion. In most of cases, the larger predator is the better competitor. The body size ratio of persisting predators (fig 4–8) ranges from  $10^2$  to  $10^6$ . Excluded competitors show either a smaller

or a larger body size ratio than this range. Body size ratio seems to be a key determinant for competition between predators, whereas predator size distribution does not show a very clear pattern (fig 4–9). Although the larger predator usually outcompetes the smaller one (but not always), some rare cases show persisting oscillations that allow persistence of both predators.

#### 4.4.5 Food chain system

A food chain is obtained by adding a top predator feeding on the former predator that becomes an intermediate predator. Many systems are able to persist through time. The body size ratio shows two interesting patterns (fig 4–10-A). First, the intermediate predator shows a lower body size ratio than previously (fig 4–5). The food chain system tends not to persist when the intermediate predator is very large compared to its phytoplankton prey. As a result, the body size ratio between the intermediate predator and its prey is centered on  $10^4$  instead of  $10^5$  in the one predator - one prey system. Second, and more surprisingly, the body size ratio between the top predator and the intermediate predator is lower (centered on  $10^2$ ) than the ratio between intermediate predator and phytoplankton, but it is consistent with existing data (fig 4–10-A). Top predator size ranges from about 1 µg to almost 1 kg (fig 4–10-B).

#### 4.4.6 Food chain system with omnivorous top predator

If the top predator can also feed on the phytoplankton prey, we obtain a food chain with an omnivorous predator. Only 2% of interactions leading to a persisting food chain (former section) lead to a persisting system when the top predator is omnivorous. These predators show a higher size ratio than intermediate predators with the shared prey (fig 4–11-A), which can be explained by the fact that omnivorous predators have to be larger than both prey species. Omnivorous top predators also show a smaller size range (fig 4–11-B) than non-omnivorous predators (from 10 µm to 10 mg instead of 1 µm to almost 1 kg to non-omnivorous predators).

#### 4.5 Discussion

The present study provides insights into predator and prey size-structures that lead to persistence of very common food web modules. A new feature is the direct relationship to concrete traits, related to size. Former studies investigated properties of trophic relationships such as intraguild predation or omnivory (Arim & Marquet, 2004; Milo *et al.*, 2002; Bascompte & Melián, 2005), or persistence of a specific module (Holt *et al.*, 1994). Other studies focused on specific topics such as the origin of compartmentalization (Guimerà *et al.*, 2010), importance of modules in a context of metacommunities (Gravel *et al.*, 2011), or indirect effects of predation (Sauve *et al.*, 2016). On the other hand, theoretical studies about predator and prey (Gellner *et al.*, 2016) often rely on abstract traits that are difficult to relate to concrete biological traits.

Our model merges the physical and the biological components of ecosystems, and it is based on concrete traits related to body size. Therefore, it provides new and easily testable hypothesis. The model does not rely on pre-existing data on food webs. It is based on basic laws of Newtonian physics and fluid dynamics, and well-known empirical size-based biological rules. Thus, the mechanism depicted in this study and the conclusions derived are valid for a wide range of predator and prey sizes. Constraints due to size and physical factors limit the available parameter space since some interactions are not feasible or sustainable.

Our study investigates how size-related constraints at the individual level lead to patterns at the community level. Four major patterns emerge. First, it seems that predator size has a major impact on the dynamics since either it leads to a single point equilibrium (small predators) or permanent oscillations of abundances (large predators). The model predicts that body size ratio between intermediate consumers and phytoplankton can be very high, but this is consistent with observed interactions. It has to be mentioned that this ratio represents phytoplankton feeders only (not predators in general). Real data show that even larger consumers exist. However, above a given size, the consumer is so much larger than the resource that it is likely to feed on more than one cell at a time (e.g., microphagy). This mechanism violates the assumptions of the model. The present model cannot predict these interactions.

Second, predator size is also the main driver for resource-competition between predators. Results from the two predators - one prey systems reveal that competition between two consumers sharing the same phytoplankton resource often leads to exclusion of the smaller consumer. Hence, the larger consumer can usually deplete the common resource population below the minimum requirement of the smaller consumer (see fig 4–2), and therefore it outcompetes the smaller one. Nonetheless, a few interactions lead to coexistence of the two consumers. When coexistence occurs, it appears that the larger consumer shows a significant decrease of its abundance when it is in mixture, compared to its abundance when it is alone (i.e., in a one predator - one prey system). Both consumer populations as well as resource population show permanent oscillations. Thus, the best consumer cannot achieve a sufficient abundance that would deplete resource availability below the minimal requirement of its competitor. It is a permanent non-equilibrium coexistence (Levins, 1979; Armstrong & McGehee, 1980).

Third, predator size is also of primary importance for prey coexistence in the one predator - two prey system, while prey size drives the outcome of prey competition otherwise. Hence, for systems where two phytoplankton species compete for the same resource (light) and are consumed by the same consumer, it appears that most of cases lead to competitive exclusion of the larger phytoplankton species. Since phytoplankton *per capita* growth rate decreases when size increases, a smaller species should be the best competitor. The presence of the consumer can sometimes regulate the abundance of the better competitor and mediate persistence of both species. Studies on predator-mediated persistence of prey (Paine, 1966; Hastings, 1978; Abrams, 1999) provided useful conclusions, but they do not consider a large range of prey sizes. Our model describes a specific type of interactions between phytoplankton and herbivore zooplankton. It may explain why the model seldom predicts persistence of this module, while it seems to be common in natural systems (Bascompte & Melián, 2005).

Fourth, the size ratio of the top predators to intermediate consumers is smaller than that between intermediate consumers and phytoplankton. This result is consistent with observed interactions. According to the model, omnivory occurs only within a relatively narrow range of predator sizes. When the top predator is omnivorous, only 2% of interactions leading to a persisting food chain (i.e., when the top predator is not omnivorous) lead to a persisting system, which is in accordance with former studies arguing that omnivory can be destabilizing and should occur within a specific range of conditions (Vandermeer, 2006; Gellner & McCann, 2016). Interestingly, omnivorous predators face a trade-off. On one hand, they are top predators and need to be larger than the intermediate predator. On the other hand, they cannot be too large, otherwise feeding on the basal prey (phytoplankton) results in negative net gains, even when the prey is very abundant. Therefore, only a narrow range of sizes allows omnivory. It is possible that if a behavioral component were added to model the system (such as an active choice by the predator), it may lead to greater persistence of these predators.

Further improvements can be proposed. The model considers only one basal resource (light), which is but one fundamental resource for primary producers. Chemical nutrients also limit the growth of primary producers, and indirectly consumers (Sterner & Elser, 2002). Adding competition for nutrients would increase the potential number of coexisting primary producers according to resource-based competition theory (Tilman, 1980; Grover, 1997). It therefore would increase the number of intermediate predators and probably the number of top predators within the same system. This would allow to move beyond exploration of simple food web modules, and potentially extend the system towards a whole food web.

In conclusion, considering the effects of physical factors from the medium and size-related traits provides new insights about the size-structure of food web modules. Our dynamical model provides a mechanistic underpinning to some well known size patterns of food webs. Using more realistic models, the present study emphasizes the need to consider the role of the surrounding medium on species interactions and the ecology of food webs (Denny, 2016).

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Symbol	Parameter	Value	Unit	Source
g	acceleration due to gravity	9.81	$\mathrm{m.s}^{-2}$	Denny (1993)
$ ho_m$	medium density	1000	${\rm kg.m}^{-3}$	Denny (1993)
$\mu$	medium dynamic viscosity	$1.35 * 10^{-3}$	$N.s.m^{-2}$	Denny (1993)
$ ho_b$	body density	1080	${\rm kg.m}^{-3}$	Denny (1993)
Re	Reynolds number		dimensionless	
$C_d$	drag coefficient		dimensionless	
$I_0$	Incident light intensity	$3.5 * 10^{-4}$	mol photons.m <sup><math>-2</math></sup> .s <sup><math>-1</math></sup>	
z	Water column depth	50	m	

Table 4–1: Physical parameters included in the model

Symbol	Parameter	Value	Unit	Source
E	Energy content		$J.ind^{-1}$	
$R_{dw}$	Dry ash-free mass over wet	0.16	dimensionless	
	mass ratio			
$E_{dw}$	Energy over dry mass ratio	23000	$\rm kJ.kg^{-1}$	
v	sinking velocity		$\mathrm{m.s}^{-1}$	
R	<i>per capita</i> net growth rate		$s^{-1}$	
P(N)	Gross photosynthetic rate		$mg C.s^{-1}$	
$C_p$	Photosynthetic cost		$mg C.s^{-1}$	
$P_{max}$	Maximal gross photosynthetic rate		mol $C.s^{-1}$	
$k_{max}$	Maximal gross photosyn-	$7.75 * 10^{-18}$	$mol \ C.s^{-1}$	Reynolds $(1990)$
	thetic rate at reference size ( <i>Chlorella</i> cell)			
$V_{0p}$	Volume at reference size for	33.5	$\mu { m m}^3$	Reynolds $(1990)$
	photosynthetic rate ( <i>Chlorella</i> cell)			
a	Absorption cross-section		$\mathrm{m}^2$	
c	Chlorophyll a content		${ m mg~chla.m}^{-3}$	
$C_0$	Carbon content at reference	$2.6 * 10^{-13}$	g C	Menden-Deuer &
	size			Lessard $(2000)$
$V_{0c}$	Volume at reference size for	1	$\mu { m m}^3$	Menden-Deuer &
	carbon content			Lessard $(2000)$
$\phi$	Quantum yield of photosyn-	0.1	mol C. mol	Kirk (1994)
2	thesis	- 10 1	photon <sup>-1</sup>	
ζ	Cost of photosynthetic appa- ratus	$7 * 10^{-4}$	mol photon. mg chla <sup>-1</sup>	Raven (1984)
au	Average lifetime of photosyn-	24	h	Riper <i>et al.</i>
	thetic apparatus			(1979)
$C_m$	Metabolic loss		$\mathrm{J.s}^{-1}$	
$l_{0d}$	Death rate at reference size	$1.58 * 10^{-6}$	$s^{-1}$	McCoy &
				Gillooly $(2008)$
$V_{0d}$	Volume at reference size for	$1.08 * 10^3$	$\mu { m m}^3$	McCoy &
	death rate		1	Gillooly $(2008)$
m	Death rate		$ind.s^{-1}$	

Table 4–2: Biological parameters for primary producers

Table 4 5. Diological parameters for predators						
Symbol	Parameter	Value	Unit			
$M_b$	body mass		kg			
$V_b$	body volume		$\mathrm{m}^3$			
$S_b$	cross-section surface of the body		$\mathrm{m}^2$			
f(N)	functional response		$s^{-1}$			
e(N)	conversion efficiency		dimensionless			
$E_p$	predator energy content		J			
$E_N$	prey energy content		J			
$R_{dm}$	ash-free dry mass to wet mass ratio	0.16	dimensionless			
$R_{ed}$	energy to ash-free dry mass ratio	$23 * 10^{6}$	$ m J.kg^{-1}$			
$C_{met}$	metabolic rate		$\mathrm{J.s}^{-1}$			
$D_{detec}$	detection distance		m			
$B_d$	bite diameter		m			
$B_s$	bite size		kg			
$B_t$	bite time		S			
$E_r$	encounter rate		$s^{-1}$			
$v_N$	prey speed		$\mathrm{m.s}^{-1}$			
$v_p$	predator speed		$\mathrm{m.s}^{-1}$			
$\dot{P_c}$	capture probability		dimensionless			
$t_s$	search time		S			
$t_c$	capture time		S			
$t_h$	handling time		S			
$C_s$	searching cost		J			
$C_{c}$	capture cost		J			
$C_h$	handling cost		J			

Table 4–3: Biological parameters for predators



Figure 4–1: Functional response according to prey size. Black curve is the larger prey, red curve is a smaller prey, and blue curve is an even smaller prey. When prey size increases, a predator becomes saturated more quickly, and reach a lower maximal response.



Figure 4–2: Zero Net Growth Isoclines (ZNGI) for prey (A and B) and predator (C and D) in the one predator - one prey system. Prey isoclines have a hump shape, while predator isoclines are straight lines. In each panel, size increases by one order of magnitude from the solid line, to the dashed line, dotted line, and dashed-dotted line. (A) Prey ZNGI shows a peak at lower abundance when prey size increases. (B) Prey ZNGI is shifted towards lower predator abundance when predator size increases. (C) When prey size increases, predator ZNGI is shifted towards lower prey abundance. (D) When predator size increases, predator ZNGI is first shifted towards lower prey abundance, then it goes on the opposite direction.



Figure 4–3: Dynamics for one predator - one prey systems. (A) Dynamics according to predator and prey sizes. Predator size is the more important determinant of what type of dynamics occur. For a given prey, consumption by small predator predominantly results in point equilibria (blue area), while consumption by a larger predator leads to persisting oscillations (red area). (B) Example of persisting oscillatory dynamic for prey (green line) and predator (black line). (C) Example of single point equilibrium dynamic: oscillations dampen down until an equilibrium value is reached for the predator and for the prey (dynamics are plotted on a logarithmic time scale to capture the long dampening period).



Figure 4–4: Sustainable predator and prey size ranges. Predator and prey sizes were chosen regularly from a size range bounded by the dashed lines. The yellow and blue areas combined show interactions leading to positive growth of the predator population for prey abundance lower than prey carrying capacity. However, only the blue area allows persistence of the predator for the dynamic model at steady state.



Figure 4–5: Predator to prey body size ratio for one predator - one prey systems: comparison between predicted ratio from the model and empirically observed data (Brose et al., 2005). Predicted body size ratio (grey box) ranges from 2 to  $10^7$  with a large part of the distribution centered on  $10^3$  to  $10^6$ . The predicted range is narrower than the observed one (white box). Due to the model's assumptions, a predator cannot feed on prey larger than itself, thus the ratio is bounded at 1 (i.e., equal size).



Figure 4–6: Distribution of predator - prey size ratios for one predator - two prey systems. Each panel shows the distribution of overall body size ratios between predators and the smaller prey (left box) or the larger prey (right box). Prey 1 is the smaller one, and prey 2 is the larger one. Percentages refer to the relative proportions of the different outcomes in the results listed on top of each panel. Most interactions lead to exclusion of the larger prey (central panel). But some interactions lead to exclusion of the smaller prey (right panel), or coexistence between both prey (left panel).



Figure 4–7: Distribution of predator body size (A) and prey body size (B) for one predator - two prey systems. Prey 1 is the smaller one, prey 2 is the larger one. Percentages refer to the relative proportions of the different outcomes in the results listed on top of each panel. (A) Predators whose interaction with the prey leads to exclusion of one prey (either the smaller or the larger) do not differ in size. Predators that allow persistence of both prey are significantly smaller than predators that are responsible for the exclusion of one prey (Mann-Whitney post-hoc test, see main text). (B) Most of interactions lead to exclusion of the larger prey. But some interactions lead to exclusion of the smaller prey or coexistence of both prey.



Figure 4–8: Distribution of predator - prey size ratio for two predators - one prey systems. Predator 1 is the smaller one, and predator 2 is the larger one. Percentages refer to the relative proportions of the different outcomes in the results listed on top of each panel. Interactions mostly lead to persistence of the larger predator. Rare cases show persistence of the smaller predator or coexistence of the two predators. For each pair, the left box represents the smaller predator, while the right box represents the larger one. Persisting predators show a ratio ranging from  $10^2$  to  $10^7$ , while excluded predators are either smaller or much larger than their competitor.



Figure 4–9: Distribution of predator body size (A) and prey body size (B) for two predators - one prey systems. Predator 1 is the smaller one, and predator 2 is the larger one. Percentages refer to the relative proportions of the different outcomes in the results listed on top of each panel. (A) Some predators can coexist, but exclusion of the smaller predator is the dominant pattern. (B) Prey sizes do not differ among the different outcomes.



Figure 4–10: Distribution of size ratios (A) and predator size range (B) for food chain systems. (A) The grey box represents the body size ratio between the intermediate consumer and its prey in a one predator-one prey system. The blue box shows the corresponding distribution for a food chain system. Within a food chain, intermediate consumers show a distribution shifted towards lower size ratios. The red box shows the ratio between top predator and intermediate consumer. The top predator has a size ratio ranging from 1.5 to  $10^6$ , which is significantly smaller than the intermediate consumer's size ratio (Mann-Whitney test). A comparison between predicted (red box) and observed (purple box) body size ratios between top predator and intermediate predator shows that the predicted range of values is very similar to the observed one (except for low ratios since the model does not allow a predators. Top predators range from 100  $\mu$ g to almost 1 kg.



Figure 4–11: Distribution of body size ratios (A) and predator sizes (B) for a food chain system with omnivorous top predator. (A) Body size ratio between intermediate predator and phytoplankton prey (blue box), between omnivorous predator and phytoplankton prey (green box), and between omnivorous predator and intermediate predator (red box). Omnivorous predators show a size ratio significantly greater than intermediate predators for the shared prey. Omnivorous predators are on average 10 time bigger than intermediate predators. (B) Size distribution of non-omnivorous top predator (red box) and omnivorous top predator (green box). Omnivorous predator size ranges from 50  $\mu$ g to 10 mg.

# Chapter 5

General conclusion

### 5.1 General discussion

In the thesis, I investigate the ways in which the discipline of ecology can gain from considering the mechanical constraints imposed on organisms by their surrounding medium. Across all ecosystems, physical factors inherent in media define the mechanical constraints imposed on every organism. The effects and nature of these constraints are mostly size-dependent. Therefore, considering the role of media yields novel insights into the size structure of communities.

It appears that phytoplankton species can persist within a size-related range of turbulence (Chapter 2). Additionally, predators can feed on a range of prey sizes (Chapter 3), and this range is bounded by a mechanical limit related to capture (upper prey size) and an energetic limit related to handling (lower prey size). Lastly, predator size plays a major role in predator-prey dynamics (Chapter 4), and persistence of food web modules.

Turbulence plays a major role for phytoplankton species, as it was explored in Chapter 2, but it may also be used to link together some themes discussed in Chapters 3 and 4. In Chapter 2, I showed that primary producers persist within a size-dependent range of turbulences. As a result, turbulence should affect the structure of food webs that are based on phytoplankton. Specifically, larger phytoplankton cells require a higher minimum threshold of turbulence for persistence than smaller cells. Therefore, smaller prey often outcompete larger ones. Hence, according to the model, one predator - two prey modules should be rare. Since smaller prey are also more likely to persist at low turbulence, this pattern should be even more dominant under this condition. Similarly, according to the model, larger predators usually outcompete smaller predators sharing the same prey. However, smaller predators can persist when the shared prey is significantly smaller, which, again, is more likely to occur at low turbulence. Thus, when turbulence is low, it should be more common for a smaller predator to outcompete or coexist with a larger predator.

Turbulence should also affect predator-prey relationships. In Chapter 3, I showed that mechanical limits constrain the range of prey on which a predator can feed. Turbulence may affect these patterns. Some studies have shown that turbulence affects encounter rates between predators and prey, especially for small species of predators (Rothschild & Osborn, 1988; MacKenzie & Kiørboe, 1995). Turbulence may affect search cost, which in turn may affect minimum predator size. Turbulence may also affect capture probability (Lewis & Pedley, 2001) for zooplankton species. It would have a strong impact on the upper size that a predator can capture, and thus the upper size that it can consume. Hence, high turbulence may increase upper prey size for small predators, which in turn may increase likelihood of a larger predator dominating a smaller predator with which it shares prey.

### 5.2 How to go further?

The models proposed in this thesis consider physical factors leading to sizerelated mechanical constraints. This thesis can be viewed as a starting point for either theoretical studies seeking more realistic hypotheses and conclusions, or empirical studies focusing on general conclusions.

## 5.2.1 Theoretical studies

Further theoretical studies may extend the models proposed within this thesis. Chapter 2 considers a relatively simple case were the water column is well mixed; therefore a natural improvement would be to consider incomplete mixing. Incorporating a wide range of phytoplankton cell sizes would represent a novel contribution to the existent phytoplankton models with thermocline (Huisman et al., 1999; Mellard et al., 2011). A more involved improvement on these models would be to consider nutrient limitation: nutrients usually show a distribution that is opposite to light availability within the water column (Yoshiyama et al., 2009). There is an interplay between light and nutrient limitation, and these two variables influence the nutritional quality of the phytoplankton (Hessen, 2008), which would in turn affect consumers, and potentially the whole food chain. Nutrients can also affect the physical properties of phytoplankton cells by changing their density, thus affecting their buoyancy (Richardson & Cullen, 1995). A model that would explicitly make connections between light, nutrients, turbulence, and cell size should provide new insights into phytoplankton persistence and aquatic ecosystems in general.

The study of food web modules (Chapter 4) could also be improved by incorporating nutrients into theoretical models. It would require the transformation of the energetic-based model presented in Chapter 4, into a stoichiometric model, where species would have size-dependent nutrient requirements (Urabe & Watanabe, 1992; Elser *et al.*, 2003). It would lead to a complex but more realistic approach to real aquatic systems, and the approach could also be extended to terrestrial systems.

## 5.2.2 Empirical studies

Although theoretical, this thesis also provides useful insight for empirical studies because it provides 1) testable hypothesis, and 2) guidance for future studies. Chapter 2 provides testable results about conditions leading to phytoplankton persistence. It would be possible to test at least some of the conclusions from the model in microcosms: using a systematic approach to size and mixing conditions. A simple experiment would require tanks deep enough to have a light zone and a dark zone. A temperature gradient would generate mixing within the water column. Then, testing several phytoplankton sizes (one species per tank) and several mixing strengths in a factorial design, it would be possible to determine the optimal range of turbulence, or at least part of it, for each species. It may also be extended to mesocosms (in lakes for example) as Huisman *et al.* (2004) did for some species.

Similarly, Chapter 3 provides strong conclusions about predator and prey sizes across ecosystems. Conclusions about the relationship between predator size and prey size ranges are relatively simple to test. The database I used to test the model already represents a significant amount of work done by many people on a large number of species (see Brose *et al.* (2005), and Hatton *et al.* (2015) for full references). However, among taxa represented in the database, some groups exhibit large variations in size. It would be valuable to compare this variance with predictions from the model, and see if some specific taxa show a greater variance than others. Our knowledge of predator and prey relationships in nature remains fragmentary. Even size measures are not totally satisfactory: many researchers measure body length (Brose *et al.*, 2005), but the relationship of body length with body mass is not always straightforward. Moreover, many studies of plankton give dry mass, carbon content, or total biomass in a given volume (Bode *et al.*, 2005; Pérez *et al.*, 2005). These measures are difficult to compare with individual (wet) body mass. Further empirical studies of predation should focus more precisely on body mass, as well as the shape variables that are of primary importance for constraints on motion. Studies like Barnes *et al.* (2008) can be viewed as a novel way to collect these data since each individual is measured, which shows the size distribution of species.

Chapter 4 provides insights into the size structure of food web modules. Many food web studies emphasize the existence of these modules within existing food webs. However, body size ratios between predators and prey have mostly been studied in the context of the whole food web, not food web modules (Dunne, 2005; Gravel *et al.*, 2013). Thus, predator and prey sizes within modules should be more clearly investigated to determine size distribution and size ratios of predators and prey. These investigations should involve a large variety of food webs and across different types of ecosystems. This implies the addition of size information to networks analysis, which has the potential to open productive avenues of food web research.

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## 5.3 General implications

This thesis emphasizes the need to consider the surrounding medium in ecological studies, since the medium plays a major role in species persistence and interactions. Both theoretical and empirical studies should pay more attention to physical factors to gain a better understanding of ecological mechanics (Denny & Gaylord, 2010; Denny, 2016). In a context of climate change, fluid properties may be modified since most properties are temperature-dependent (Denny, 1993). An increase in temperature may lead to modifications of the thermocline properties in aquatic systems (Winder & Sommer, 2012). These modifications will have major impacts on mixing regimes, nutrient availability, and ultimately on community composition. The present thesis provides a new framework to investigate community structure and dynamics, and this framework should be pursued even further.

This thesis focuses on individual-based processes that ultimately lead to community-level patterns. At the individual level, biotic processes (biological rules) and abiotic processes (mechanical laws) constrain individual growth, and interactions between organisms. By linking processes to species interactions, my thesis also draws connections between community ecology and ecosystem ecology. These two major fields of ecology have developed mostly independently for decades (Loreau, 2010a). Approaches which simultaneously consider biotic and abiotic factors, energy flow, and species interactions should be viewed as a step towards unification in ecology (Loreau, 2010b).

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## APPENDIX

## A Chapter 2 unpublished material: consequences for interspecific competition

Chapter 2 considered only one species at a time, where individuals show intraspecific competition for light. These results can potentially be extended for interspecific competition.

## A.1 Relationship between turbulence and body size, and consequences for competition

Turbulence, represented as diffusion, plays a major role in species persistence. Hence, it should play a role in competition between two species of different body sizes. However, the relationship between current speed and diffusion rate according to body size is mainly unknown. The approach used throughout the whole chapter assumes that turbulence has similar effects on phytoplankton cells of different body sizes. In this additional work, this approach is used as a null model. However, studies on particle motion tend to demonstrate that particles diffuse more as their size decreases (Friedlander, 2000). Thus, assuming that a given current has a similar effect on a very small species and a large species might be wrong. Hence, we also propose an alternative model considering that a small cell should accelerate more than a large cell. Therefore, a large cell should have a lower diffusion rate than a small cell. In this section, the two models were tested. The first model is a null model considering that all species have the same diffusion rate for a given current strength. This model has been tested in a twospecies competition situation, with two species of different body size and for different turbulence strengths. This leads to the following results. First, when turbulence allows both species to persist on their own, the smaller competitor always outcompetes the bigger one. Second, when turbulence strength allows only one species to persist on its own, this species is always the smaller one. The inverted situation (i.e. the larger species is able to persist on its own, while the smaller one is not) never occurs (fig. S.1).

The second model assumes that, for a given current speed, small species have a higher diffusion rate than larger species. In this model, for each diffusion value tested, the diffusion parameter of the bigger competitor is decreased by a factor k. In that situation, two cases occur (fig. S.1). We find that, if the smaller species is able to persist on its own, it always outcompetes the larger species. Second, a given turbulence strength can allow the larger species to persist but not the smaller species. The reverse situation leads to the opposite outcome. In summary, the smaller competitor always outcompetes the bigger one if this small species is able to persist. If k is strong enough, the larger species optimal range of turbulence is shifted out of the smaller species range of turbulence. Therefore, the larger species can persist, while its competitor cannot.

## A.2 Size-mediated persistence and its consequences for interspecific competition

The null model patterns can be explained by comparing behavior of population throughout a wide range of diffusion rate. First, within the range of turbulence allowing persistence of both species, the *per capita* population growth rate plays a major role. Because *per capita* population growth rate decreases with increasing body size, the smaller species is always more productive than its competitor. Moreover, the smaller species is always closer to the surface since it sinks more slowly, and thus this species shades its competitor. Second, only the smaller species should obviously persist when diffusion strength allows the persistence of the smaller species but not the persistence of the larger species, but the reverse situation is impossible because the range of diffusion strengths that allows persistence decreases with body size, such that the range of the bigger competitor is entirely embedded within the range of the smaller species (see fig. 2–1 and S.1). Hence, the outcome of competition will always be the same: the smaller species will outcompete the larger species. Coexistence or even a switch in the competition outcome is unlikely if species diffuse at the same rate.

The alternative model leads to the similar conclusion that the smaller species outcompetes its bigger competitor when it is able to persist on its own. But this model also allows cases where the bigger competitor persists on its own, while the smaller species goes extinct (figure S.1). These patterns can be explained again by the range of turbulence that allows persistence of the various species. In this alternative model, the range of turbulence allowing persistence of the larger species is shifted towards higher levels of turbulence, and therefore is not totally embedded within the range of turbulence allowing persistence of its competitor. Two zones of turbulence strength can be found. The first one, at low turbulence strength, allows persistence of the smaller species. In that zone, the bigger competitor is either unable to persist on its own or is excluded by the smaller species (as explained above). The second zone allows persistence for the bigger competitor but not for the smaller one, which leads to persistence of the bigger competitor. Hence, a size-related difference in how species diffuse in response to turbulence does not switch the outcome of competition when both species persist, but creates a range of turbulence values where the persistence of the larger species is promoted, while the smaller species diffuses too much and goes extinct. Therefore, this alternative model does not really allow a switch in competitive outcome. In fact, it creates new conditions within which the bigger competitor can persist, but not the smaller one.

## A.3 Conclusion

This alternative model seems a promising way to explore interspecific competition between phytoplankton species. However, it needs some improvement. So far, the model considers only light as a limiting resource. This assumption is perfectly justified for a bloom period, where nutrients are fully available, but competition between species would probably require a longer time scale to consider. According to population abundances predicted by the model, nutrients would become limiting. Thus, the model should include the effects of nutrient limitation as well as light limitation. It seems a promising topic to study in the future.

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## **B** Estimation of some size-related parameters

One of the goal of this thesis is to provide more realistic models based on concrete, measurable traits. Whenever possible, parameters are related to body size to account for the variations of size on species interactions. Some parameter values were directly taken from existing literature, while other values were derived from data. Last, some values needed to be calibrated. Parameter values directly coming from existing literature are cited in the corresponding chapters. Here, I explain how the remaining parameters were estimated or calibrated.

## **B.1** Sinking velocity

Sinking velocity describes how fast an individual body sink within the water column. But it also describes how fast an individual body falls within air column (by replacing water density and viscosity by air density and viscosity). This velocity is used in chapter 2 (advection term) and in chapter 4 (sinking rate of primary producers).

The calculation is done using mechanical laws. Three forces constantly apply on organisms. The first force is weight due to gravity; it is oriented downwards. The second force is Archimedes' force due to medium density; it is oriented upwards. The last force is drag due to medium density and viscosity; it is always opposed to motion (thus, oriented upwards in that case). Within this thesis, only surface drag was considered. The forces lead to an overall sinking force (F).

$$F = gM_b - V_b\rho_m g - \frac{1}{2}S_b v^2 \rho_m C_d \tag{B.1}$$

where  $M_b$  is body mass, g is acceleration due to gravity,  $V_b$  is body volume,  $S_b$ is the body section surface,  $\rho_m$  is medium density, v is speed, and  $C_d$  is the drag coefficient. Considering Newton's second law, force divided by mass represents acceleration, which is the first derivative of speed by time.

$$\frac{dv}{dt} = g - \frac{V_b \rho_m g}{M_b} - \frac{1}{2} \frac{S_b v^2 \rho_m C_d}{M_b}$$
(B.B.1)

The sinking velocity is assumed to be an equilibrium speed, when all the three forces compensate each other (i.e., acceleration is null). Due to the recursive relationship between speed and drag, the sinking velocity at steady state is calculated by numerical approximation using the bisection method (Burden & Faires, 2011). Since within this thesis, this parameter mostly applies on phytoplankton cells, it has been calibrated using measured sinking rates of phytoplankton cells (Reynolds, 2006). This method seems to be more accurate than Stockes' approximation (fig. S.2).

## **B.2** Carbon content

Phytoplankon growth needs light. Photosynthetic rates usually are in mol  $C.s^{-1}$ . In order to transform these molar rates into *per capita* rates, they are first multiplied by the molar weight of carbon (12 g. mol  $C^{-1}$ ), which leads to a rate in g  $C.s^{-1}$ . Then, these rates are divided by the amount of carbon needed to build one individual. Thus, a parameter accounting for carbon content per cell is needed. This parameter was estimated from data (Menden-Deuer & Lessard, 2000).

$$C_b = C_0 \left(\frac{V_b}{V_{0C}}\right)^{0.88} \tag{B.2}$$

where  $C_0$  is carbon content at reference size, which is set at 2.6 \* 10<sup>-13</sup> g C, and  $V_{0C}$  is volume at reference size, which is set at 10<sup>-18</sup>m<sup>3</sup> (fig. S.3).

## B.3 Death rate

Death rate is assumed to be inverse of the lifespan. Lifespan is known to scale with body size (Peters, 1986). Death rate has been calibrated using empirical data (McCoy & Gillooly, 2008).

$$l_d = l_{0d} * \left(\frac{M_b R_{dw}}{V_{0d}}\right)^{-0.22}$$
(B.3)

where  $l_d$  is death rate,  $M_b$  is body mass, and  $R_{dw}$  is the ratio between the dry ash-free mass and the wet mass.  $l_{0d}$  is death rate at reference size, which is set at  $1.58 * 10^{-6} \text{ s}^{-1}$ , and  $V_{0d}$  is reference size, which is set at  $1.08 * 10^{-15} \text{ m}^3$  (fig. S.4).

## **B.4** Detection distance

Each predator detects a prey within its detection sphere, whereas each prey detects a predator closer than the detection distance of this prey (see chapter 3). As body size increases, an individual should have a larger detection sphere. Detection distance was estimated using a model provided by Pawar *et al.* (2012).

$$D_{detec} = d_0 \left(\frac{M_b}{M_{0d}}\right)^{\frac{1}{3}} \tag{B.4}$$

where  $D_{detec}$  is detection distance,  $d_0$  is the detection distance at reference size, which is set at 0.225 m,  $M_{0d}$  is the reference mass, which is set at 0.0376 kg (fig. S.5).  $d_0$  and  $M_0$  were estimated by regression from Pawar *et al.* (2012) (supplementary material).
## **B.5** Bite diameter

The time needed to consume a prey depends on the bite size. Hence, bite size determines how many bites will be needed to consume the prey. Bite size scales with body mass. Several slopes can be derived from data (Wilson & Kerley, 2003). The intermediate one was chosen.

$$B_d = B_0 \left(\frac{M_b}{M_0}\right)^{0.32} \tag{B.5}$$

where  $B_d$  is bite diameter,  $B_0$  is bite diameter at reference size,  $M_b$  is body mass, and  $M_0$  is body mass at reference size. A regression was performed on the data points with the aforementioned slope (fig. S.6). Reference bite diameter and reference mass were taken from the point that is the closest from the regression line.

## C Implementation of the Crank-Nicholson scheme

The model developed within chapter 2 uses an integro-reaction-advectiondiffusion equation representing changes in abundance of a phytoplankton population ( $\omega$ ) at each depth z of a water column of maximal depth  $z_{max}$ . This population has a growth term (R), a loss by sinking at a size-related velocity (v), and a diffusion term (D) due to turbulent mixing.

$$\frac{\partial \omega}{\partial t} = R\omega - v\frac{\partial \omega}{\partial z} + D\frac{\partial^2 \omega}{\partial z^2} \tag{C.1}$$

For z = 0 and  $z = z_{max}$  (i.e., boundaries), a zero-flux boundary condition is applied (i.e., Robin's boundary condition).

$$v\omega - D\frac{\partial\omega}{\partial z}|_{z=0} = v\omega - D\frac{\partial\omega}{\partial z}|_{z=Zmax} = 0$$
 (C.2)

Several methods exist to solve such a system. We decided to use a finite volume method: the water column is divided into n identical volumes. Equation C.1 can be represented in a matrix form:

$$\frac{\partial \omega}{\partial t} = \begin{pmatrix} x_0 & x_0 & & & \\ x_1 & x_1 & x_1 & & \\ & x_2 & x_2 & x_2 & \\ & & x_3 & x_3 & x_3 & \\ & & & \ddots & \ddots & \\ & & & & x_n & x_n \end{pmatrix} \begin{pmatrix} \omega_0 \\ \omega_1 \\ \omega_2 \\ \omega_3 \\ \vdots \\ \omega_n \end{pmatrix} + \begin{pmatrix} R_0 & & & & \\ R_1 & & & \\ & R_2 & & \\ & & R_3 & & \\ & & & \ddots & \\ & & & & R_n \end{pmatrix} \begin{pmatrix} \omega_0 \\ \omega_1 \\ \omega_2 \\ \omega_3 \\ \vdots \\ \omega_n \end{pmatrix}$$

The first term on the right hand side represents vertical motion (i.e., advection and diffusion), while the second term represents growth (i.e., reaction). At each depth

z, a considered volume sends individuals to the volume located below it (z + 1)by sinking and diffusion. It also sends individuals to the upper volume (z - 1)by diffusion. The focal volume receives in return individuals coming from volume z - 1 by advection and diffusion, and from volume z + 1 by diffusion. Population within this volume also shows growth (positive or negative) depending on light availability. The above matrix system can be written more simply:

$$\frac{\partial\omega}{\partial t} = A\omega + B\omega \tag{C.3}$$

where matrix A represents vertical motion of individuals, and B represents growth.

The Crank-Nicholson algorithm provides an implicit calculation of abundance within a given volume at a given time (Najafi & Hajinezhad, 2008). For any volume z:

$$\frac{\omega_{t+1}^z - \omega_t^z}{\Delta t} = A \frac{\omega_{t+1}^z + \omega_t^z}{2} + B \frac{\omega_{t+1}^z + \omega_t^z}{2}$$
(C.4)

Multiplying both sides by  $\Delta t$  gives:

$$\omega_{t+1}^z - \omega_t^z = \frac{\Delta t}{2} A \left( \omega_{t+1}^z + \omega_t^z \right) + \frac{\Delta t}{2} B \left( \omega_{t+1}^z + \omega_t^z \right)$$
(C.5)

and rearranging:

$$\left(1 - \frac{\Delta t}{2}A - \frac{\Delta t}{2}B\right)\omega_{t+1}^{z} = \left(1 + \frac{\Delta t}{2}A + \frac{\Delta t}{2}B\right)\omega_{t}^{z}$$
(C.6)

Or:

$$M_1 \,\omega_{t+1}^z = M_2 \,\omega_t^z \tag{C.7}$$

Thus:

$$\omega_{t+1}^z = M_1^{-1} M_2 \,\omega_t^z \tag{C.8}$$

Where:

$$M_1 = 1 - \frac{\Delta t}{2}A - \frac{\Delta t}{2}B$$
$$M_2 = 1 + \frac{\Delta t}{2}A + \frac{\Delta t}{2}B$$

Matrices A and B are discretized for space as follows:

$$\forall z \in ]0, z_{max}[$$

$$\frac{\partial}{\partial t}\omega_z = \left(\frac{v}{\Delta z} + \frac{D}{\Delta z^2}\right)\omega_{z-1} - \left(\frac{v}{\Delta z} + \frac{2D}{\Delta z^2}\right)\omega_z + \frac{D}{\Delta z^2}\omega_{z+1} + R_z\omega_z \qquad (C.9)$$

At the boundaries:

$$\frac{\partial}{\partial t}\omega_0 = -\left(\frac{v}{\Delta z} + \frac{D}{\Delta z^2}\right)\omega_0 + \frac{D}{\Delta z^2}\omega_1 + R_1\omega_0 \tag{C.10}$$

$$\frac{\partial}{\partial t}\omega_{Zmax} = \left(\frac{v}{\Delta z} + \frac{D}{\Delta z^2}\right)\omega_{Zmax-1} - \frac{D}{\Delta z^2}\omega_{Zmax} + R_{Zmax}\omega_{Zmax}$$
(C.11)

Therefore, A is an n by n sparse matrix, and its diagonal:

$$x_{ii} = -\frac{v}{\Delta z} + \frac{2D}{\Delta z^2} \tag{C.12}$$

$$x_{ii_{\pm 1}} = \frac{v}{\Delta z} + \frac{D}{\Delta z^2} \tag{C.13}$$

$$x_{ii_{-1}} = \frac{D}{\Delta z^2} \tag{C.14}$$

B is a diagonal n by n matrix, where each value on the diagonal is the growth term *per capita* within the corresponding volume. At each iteration, matrix B is computed to account for changes in light availability that affects growth, whereas coefficients in matrix A remain unchanged since diffusion is assumed to be constant through time.

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Figure S.1: Comparison of turbulence thresholds between a small competitor  $(1\mu m^3)$  and bigger competitors. Straight line represents the upper turbulence threshold for the small competitor. Dotted lines represent upper and lower thresholds for the other species. The top panel (A) represents competition conditions where all species diffuse at the same rate, while the bottom panel (B) represents conditions where bigger competitor diffuses 15 times less than the small competitor. In zone I, neither species can survive. In zone II and IV, only the small competitor is able to persist. In zone III, each species should be able to persist when alone, but a small competitor always excludes a larger species. In zone V, the small competitor is not able to persist, but a larger species is still within its optimal range of diffusion, and can persist.



Figure S.2: Sinking velocity as a function of body size. Points are data from literature, the solid red line is the predicted sinking velocity from the model. The solid blue line is the predicted sinking velocity when Stockes' approximation is used. The model used throughout the thesis gives more accurate predictions.



Figure S.3: Carbon content as a function of body size. Points are data from literature, the solid line is the regression line.



Figure S.4: Death rate as a function of body size. Points are data from literature, the solid line is the regression line. The red point is the point used as reference body size and reference death rate.



Figure S.5: Detection distance as a function of body size. Points are real data, the solid line is the regression line with imposed slope from literature. The red point is the point used as reference body size and reference detection distance.



Figure S.6: Bite size as a function of body size. Points are real data, the solid line is the regression line with imposed slope from literature. The red point is the point used as reference body size and reference bite size.